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THE PHYTOSOCIOLOGY OF BOREAL CONIFER—HARDWOOD FORESTS OF THE GREAT LAKES REGION¹

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INTRODUCTION

The forests centering on the Great Lakes, have contributed to the rapid settlement and development of the North American continent, to an extent which can be considered to equal the importance of the great waterway itself, the largest chain of freshwater lakes in the world. In this regard the northern sections of this forest complex, in which the boreal forests of spruce and fir converge upon the forests of the south composed of deciduous elements, have played as important a role as the southern types.

During the mid and late 19th century, economic and academic interests in these forests were intensified and local studies were initiated and descriptive accounts began to accumulate. One of the difficulties inherent in these efforts was the time-consuming nature of methods available for survey. This factor added to the inaccessibility of vast areas prevented any single worker from expanding his conception of the entire forest complex. These restrictions well explain the fact that early interpretations were limited and that such were reflected in the classification treatments which were put forth.

Recently, during the course of phytosociological analyses in a portion of the Great Lakes forest complex in Wisconsin (Curtis & McIntosh 1951; Brown & Curtis 1952), the broad relationships of various sections were indicated. As data were accumulated for various communities it became increasingly evident that a fuller understanding of the structure, dynamics and integration of these communities was

only to be obtained by traveling farther afield into adjacent areas. With the completion of the northern conifer-hardwood studies (Brown & Curtis 1952) it was clear that there existed a need for further work to elucidate the relation of northern Wisconsin types especially those associated with the boreal forest.

Since the northern forests of the Lakes region had never been sampled quantitatively over any extensive area and since the recent development of rapid survey methods permitted the coverage of relatively broad areas, the study of the boreal conifer-northern hardwoods in northern Wisconsin was expanded into adjacent states and Canada. It was hoped that the project would also expand our knowledge of the true nature of the Great Lakes forests.

The lack of quantitative literature on the adjacent boreal forests emphasized the need of a quantitative analysis in the area where the great mass of these forests becomes confluent with that of the deciduous forests. This confluence has resulted in forests of considerable complexity and it was considered that information gained here might be profitably employed in future research to understand the Canadian boreal forests.

With such considerations in mind, a search encompassing almost the entire area of the northern Great Lakes region was made during the period 1954-1957 in an effort to find suitable stands for the present study.

LITERATURE REVIEW

The botanical aspects of the Great Lakes region were first described by the early missionaries and explorers beginning in the 1600's. Naturally, these

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papers as well as many others which have followed were of a descriptive nature, and have adequately portrayed the vegetation in its broad general aspects. Unfortunately, the few accounts based on quantitative investigations have commonly dealt with relatively small and localized areas. However, far-reaching conclusions have often been derived from either these general descriptions or local investigations, and claim has been laid as to their adequacy in fully interpreting the nature of the entire forest complex. A complete review of this abundant literature, both historical and recent, is available (Maycock 1957).

The most outstanding historical paper dealing with these forests is that of Sargent (1884) who referred to the area, silvically, as the Northern Pine Belt. His comments pointed to the transitional nature of the communities of this region. *Pinus strobus* was used to characterize this area because of its broad range, throughout, which knit together a group of heterogeneous tree distributions, but primarily because it was the most desirable and sought after lumber species. His reference to a great number of tree distributions indicates a delimitation of the forest type on the basis of floristics rather than distinctive community structure. He seemed to be describing a floristic province. The fact that he relied heavily in this respect upon a widely distributed, economically valuable species, bore no relationship to any climactic characteristics of that species, yet 45 years thence his treatment was cited as the basis for recognition of a supposedly distinct climax formation (Clements 1916). Harshberger (1911) referred to these forests as standing midway between the deciduous forests of the central and eastern United States and the subarctic forests.

The boreal, deciduous and pine-hemlock forests of the Great Lakes were extensively considered by Weaver & Clements (1929). As a consequence of glaciation, subsequent migration and competition, the barrier of the lakes and the fact the region is marked by climatic extremes, they claimed there has resulted the inclusion of many small relict areas of pine, hemlock, or both, well within the mass of deciduous or boreal forest. In discussing the nature of climax in the region Clements (1916) postulated that all climax dominants need be of the same major life form, indicative of a similar response to climate. This concept is apparently agreed upon by many ecologists but his additional *a priori* assumption that evergreen trees might not be regarded as proper dominants of deciduous forest, has led to great strife and controversy among vegetational ecologists, both Clementsian and otherwise. Thus, when he came to classify the vegetation of the lakes region he was left no choice and of consequence was forced to establish a separate formation, his "Lake Forest."

These forests were thoroughly evaluated by Nichols in 1935. He appeared to favor treating vegetation as he encountered it in the field and his interpretation was therefore unhampered by finding *Tsuga canadensis*, *Pinus strobus* or *Picea glauca* and *Abies balsamea* growing with hardwood species. "A

mesophytic forest comprising a mixture of evergreen coniferous and deciduous broadleaf trees," was described as the climatic climax. His conceptions of the climax composition and structure of these forests, their transitional and continuous nature and the regional importance of various components agree well with many of the current conceptions held.

A group of investigators, Cooper (1913), Bergman & Stallard (1916), Lee (1924), Weaver & Clements (1929), Grant (1934), Nichols (1935), Kell (1938), Drexler (1941), Buell & Gordon (1945), Braun (1950), Butters & Abbe (1953), Oosting (1956), at one time or another and as the outcome of either local or extensive studies have appeared to favor a *Picea-Abies*; *Abies-Picea*, or some association of definitely boreal tree species, as the climax forests for either local or broad areas of the Great Lakes region. This line of thought can be ultimately traced to the appearance of Cooper's paper on the vegetation of Isle Royale in Lake Superior in 1913. This is of course in contrast to those who have similarly favored terminal forests composed predominantly of hardwood deciduous species with or without pine: Gates (1912), Gleason (1924), Darlington (1930), Grant (1934), Kittredge (1934), Nichols (1935), Eggler (1938), Hosie (1938), Kell (1938), Graham (1941), Potzger (1946), Braun (1950). Although many of these authors had very fixed concepts concerning the terminal forests of the region, many of them had fairly plastic ideas and favored deciduous forests or coniferous communities locally or climax forests in which both boreal and deciduous elements were mingled in mutual toleration.

The hemlock-white pine-northern hardwoods region of Braun (1950) was characterized "by the pronounced alternation of deciduous, coniferous and mixed forest communities." *Acer saccharum*, *Fagus grandifolia*, *Tilia americana*, *Betula lutea*, *Tsuga canadensis* and *Pinus strobus* represented the climax dominants in the region as a whole, "but not all occur in all parts." *Picea glauca* and *Abies balsamea* were thought of as important members toward the northern limits. Boundaries were ill-defined due to encroaching southern species and retreating northern species, "a region of interpenetrating climaxes . . ." While Braun appears to speak in terms of the independent ranges and importance of component dominants when referring to "interpenetrating climaxes," Dansereau (1944) working farther east but in an analogous vegetational situation refers to the ranges and importance of distinct associations with respect to interpenetrating climaxes. These are clearly distinct and different conceptions of the merging and intermingling tendencies of the components in this controversial vegetation of the Great Lakes.

Northward from the area under consideration the elements of the deciduous forest become more sparse until they are completely replaced by what are considered boreal elements. Similarly in a southward direction the reverse situation prevails, with the broadleaved deciduous components becoming the predominant forest residents. Hundreds of other asso-

iated species appear to be affected independently by similar fluctuations in their relative importance in the structure of the community at any one place, and ecologically play no less an important role than the dominant species. Such a conception of the forests of the Great Lakes area is to be found in many of the papers on the subject but few of the authors have considered the overall environmental conditions which have effected this vegetational situation to the extent that the quantitative aspects of the species themselves might yield some reasonable and ecologically profitable manner of treating the community.

Two studies in adjacent regions have utilized this conception of vegetation as a means of investigating the plant cover of an extensive area. Brown & Curtis (1952), in the northern pine-hardwoods in Wisconsin, found that such an approach indicated one community complex, forming "a continuum, with a continuously varying series of species which matched all segments of the full range of environments of the region, with no large group bunched in the same environment and no environments devoid of the adapted species." Although the southern deciduous hardwoods of the same state were similarly but independently investigated by Curtis & McIntosh (1951), the results were exactly similar and the terminal forests of both northern and southern communities were inseparably related. The present treatment followed closely the lines of these investigations and therefore the question was posed as to whether the northern pine-hardwood forests would bear the same kinship to the mixed boreal conifer-hardwood forests of the adjacent Lakes region and thus lead to the ultimate conclusion that, all these vegetational divisions are so interwoven and integrated as not to be amenable to classification treatments (McIntosh 1958).

DESCRIPTION OF THE REGION

LOCATION

In the course of the field work, the vegetation of an area stretching for approximately 1000 mi from Itasca Park in Clearwater County, Minnesota eastward to Algonquin Park in Haliburton County, Ontario, was examined. The north-south distribution of

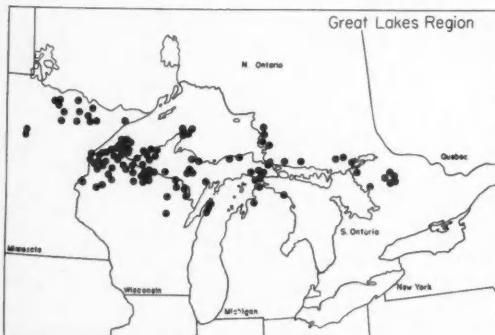


FIG. 1. The distribution of the 110 forest stands sampled in the northern Great Lakes region.

this vegetational belt was approximately 200 mi in width, between Kabetogama, Minnesota and Agawa, Ontario, the most northern points and Neopit, Wisconsin and Alpena, Michigan, the southernmost locations. Over 10,000 mi were traversed in an effort to find suitable stands. The location of stands is provided in Fig. 1.

GEOLOGY

Much of the Great Lakes area, notably the northern section, forms a part of the great Canadian Shield. The broad band of boreal conifer-hardwood vegetation under consideration corresponds roughly with the southern margin of the Shield where older Precambrian bedrock is overlain by younger Paleozoic rocks of the Mississippi valley.

The bedrock geology of the Lake Superior region has been extensively reviewed by Van Hise & Leith (1911). The whole shield, while uplifted in Pliocene time (Cooke 1947), was warped, faulted, intruded, eroded, and considerably changed. As a result, although composed largely of granite or granitic gneiss, widely scattered over its surface are irregular patches of volcanic and sedimentary rocks. The extensive limestone areas of the Niagara escarpment constitute a comparatively large percentage of the area, especially toward the southern boundary.

While these markedly different bedrock types have undoubtedly given rise to widely differing soil types, in turn affected by the great period of uplifting referred to, both considered together were probably no more influential in modifying the environment for plant life than were the changes produced by the ice advances of the Pleistocene.

have been treated by Thwaites (1950) and Flint

The progress and patterns of the glacial period (1947) and will not be reviewed here. It should be emphasized that the gigantic effects of glaciation on the forests of spruce-fir which immediately reinvaded with their retreat (Potzger 1953), and on the forests of boreal conifer-hardwoods which were successors or associates, are pertinent to any discussion of their present structure and relationships. The question of whether these forests would exist at all in their present state in the absence of glaciation can well be contemplated.

It should be sufficient to indicate that spruce-fir and spruce-fir-mixed hardwood forests in the lake region are apparently not confined to any particular geological stratum. Stands of similar composition occur throughout the region on all types of bedrock, including granites, sandstones and limestones. Nor do they appear to be correlated with drift deposits of any of the various substages of the Wisconsin glaciation.

SOILS

The lack of vegetational correlation with bedrock and drift types is equally true of soils. In the literature, arguments are often put forth to favor a close correlation between the distribution of forest units and recognizable soil types (Wilde & Leaf 1955).

These conclusions have usually been based on studies of small local areas and few stands, and they may seem reasonable in the situation at hand. The stands utilized in this study occurred on almost all soil types of the region, including sands, sandy loams, loams, clay loams, clays, peats, rock outcrops and shallow soils of many descriptions. Often stands with very similar tree composition might be situated on very different soils in the same vicinity, although the opposite may also have been true. One factor appeared to be common to all sites: soils were invariably true podsols or of a podsolic nature. Whether the podolic nature of the soils is a factor in the distribution of this type of vegetation, a result of the vegetation, or both, can well be debated.

Litter types varied similarly through the entire range from deep mor to mull. In most instances an A₁ layer was scarcely detected, making the collection of soil samples difficult, and the A₂ layer varied from gray siliceous layers up to 6 or 8 in. in thickness, to those where gray grains were barely noticeable.

CLIMATE

The lakes region in general is characterized by snowy winters and plentiful, well-distributed summer rains, a climate which greatly favors a forest vegetation. Snow depths in general, are greater here than in any other areas of the eastern half of the continent. Snow depth plays an important role in the resulting environmental conditions produced for forest growth since it is usually sufficiently deep to protect the soil from frost penetration to any great depth. A reliable impression of the general climate of the area may be found in isolineal maps for the United States (U.S.D.A. 1941) and for northern (Chapman 1953) and southern (Putnam & Chapman 1938) Ontario.

No correlations of climate with distribution of forest types will be attempted but a few of the prominent climatic factors should be reported. As one would expect, temperatures decrease northward but the differences between the northern and southern areas as a whole are not great. The differences are greater for winter (0° - 15° F average January temperature) than for summer (60° - 65° F average July temperature) periods. The trends in length of the frost-free period are fairly marked between north and south (80-130 days) although this factor varies considerably locally, and this is no doubt an important consideration in the increasing change to the evergreen habit. In general, average annual precipitation increases in an easterly direction (34" at Algonquin) from the prairie edge (25" at Itasca) and decreases northward. This latter tendency is balanced somewhat by a corresponding decrease in evapo-transpiration. Annual snowfall is greatest in the central lakes area (150") and decreases with increasing distance from this center.

POSTGLACIAL HISTORY

In the light of sparse fossil evidence of present day or closely related boreal species in the areas north

of the greatest extent of recent glaciation, botanists may well consider whether forest invasion or forest reinvasion occurred with the recession of the ice. Since the spruce-fir formation exists as it does today, dependent upon continuous disturbance and perhaps originally almost entirely upon the effects of and the conditions produced by glaciation, a question certainly exists as to whether it was previously the entity it is at present.

No centers from which the northward postglacial invasion of species occurred have as yet been definitely established. That the various great ice lobes may not have merged on all fronts is attested by the Driftless Area in southwestern Wisconsin, and by comparatively minor accumulations of drift with no other evidences of glacial action (Coleman 1926) in the regions north of Lake Superior and elsewhere. Plants may have survived in such areas. As more is learned of the effects of the ice mass on vegetation in areas directly south of it, and the persistence of species in close proximity to ice floes at present, the survival of vegetation in small patches engulfed by ice may become of greater consideration in interpreting post-glacial forest invasion.

Various areas of the Canadian Shield have been open to plant invasion for different periods of time. The last great ice advance in Wisconsin occurred some 11,000 or 12,000 yrs ago according to radiocarbon analyses of timber in the forest bed at Two Creeks, Wisconsin (Arnold & Libby 1951). Radiocarbon datings by Zumberge & Potzger (1955) indicate that Lake Algonquin began to recede about 8500 yrs ago at the time the North Bay outlet became ice-free. Datings of organic peat from a bog in the James Bay area of Quebec (Potzger 1954) indicate that a period of 2300 yrs had elapsed since the initiation of organic deposition and doubtless the occupation of the uplands by forests.

All the pollen studies conducted in the northern lakes region and northward, to the writers' knowledge, have indicated the first tree invaders were *Picea* and *Abies* (Potzger 1943, 1946, 1953, 1954; Wilson 1937; Potter 1947).

Braun (1950) claimed the hemlock-hardwood and spruce-fir-hardwood forests of the Lakes area and northeast, together with the western representatives in Minnesota, illustrate a progressive expansion and migration from a Pleistocene refugium in the northern Allegheny Mountains and the Allegheny Plateau.

GENERAL VEGETATION

A general impression as to the type and variety of vegetation in this region is obtainable in the abundant literature. In addition to extensive agricultural development throughout, much of those portions which were left in timber have been cut-over and burned. As a result, by far the greater proportion of the current forest vegetation consists of *Populus tremuloides*, *Betula papyrifera*, or *Pinus banksiana*, or mixtures of any or all of these. More advanced vegetational stages are represented by hardwoods, spruce-fir, or again, various mixtures of both. It

should be emphasized that predominantly spruce-fir stands did occur toward the southern edge of the area and stands of pure hardwoods were, in many locations, well developed in the north.

Extensive stands of *Pinus strobus* or *P. resinosa* or mixtures of both were often a noticeable segment of the landscape. With respect to mixtures of hardwoods and coniferous species, southward the conifers were usually *Pinus strobus* and *Tsuga canadensis* with much smaller representations of *Picea glauca* and *Abies balsamea*, but with increasing distance northward the latter species became the predominant conifers. The niches of fallen logs, uprooted tree pits, and other disturbed gap areas, usually occupied by *Tsuga* in the south, become progressively more favorable for *Picea* and *Abies* invasion northward. Almost any variety of stand composition resulting from combinations of any of the tree species, either in mixtures or in pure stands, is encountered in the Lakes region.

At Itasca Park the spruce-fir types are not too distant from the prairie edge and a significant number of prairie or forest edge species establish themselves in understories. One of the suitable areas for the development of these forests is located in the Littlefork Valley in northeastern Minnesota. Here *Picea glauca* and *Abies balsamea* attain considerable diameter as do *Populus* spp. and *Betula papyrifera*. In the rock outcrop areas around Ely and Gheen, *Picea* and *Abies* are more scattered, being mixed with *Pinus strobus* and *P. resinosa* on higher ground. They do grow in more dense stands on slopes leading to small drainage outlets with *Thuja occidentalis*. Along the north shore in Minnesota, spruce-fir is sparse south of Tofte, with large specimens being restricted in ravines. North of this area the type is of frequent occurrence, especially on burned over areas. In the hilly areas north of Tofte and the lake, old growth mixed conifer-hardwoods are abundant.

In Wisconsin *Abies balsamea* and *Picea glauca* are distributed over the northern half of the state, from Marathon County north. The first small stands of *Abies* are found north of Wausau and although single specimens or small isolated groups of *Picea glauca* are widespread, spruce-fir cannot be said to form a recognizable portion of the vegetation until the northern tier of counties and adjacent northern Michigan is reached. The northern sections of Douglas, Bayfield and Ashland counties support the only significant areas of spruce-fir in Wisconsin. This same area was similarly forested at the time of the land survey and is so indicated on early vegetation maps. Large specimens of *Picea glauca* and *Abies balsamea* occur along draws and streams and younger spruce-fir stands appear along the Superior shore. In this and other parts of the northern half of the state, *Abies balsamea* is widespread as an understory intrusive or as isolated large specimens with or without *Picea glauca*, in the hardwoods. At the extreme southern limits of spruce-fir on the Door peninsula in the vicinity of Bailey's Harbor, *Picea glauca* and *Abies balsamea* form impressive stands on limestone

outcrops. A similar situation prevails at the southern edge of spruce-fir on the twin Bruce peninsula in Ontario (Klugh 1912). Along the shores of Lake Superior in Minnesota, Wisconsin and Michigan, large specimens of *Pyrus americana* are often associated with these species.

In Michigan, in Gogebic and Ontonagon counties, young stands of spruce-fir are of frequent occurrence as are *Picea glauca* and *Abies balsamea* as intrusives in the understories of *Populus* stands, as well as scattered through hardwood stands. The Poreupine Mountain area supports many old growth hardwood stands with *Abies balsamea* and *Picea glauca* as somewhat minor associates. These species become of greater importance here in similar stands on areas of high water tables, or in spring-fed situations. The Keweenaw peninsula and Houghton, Baraga and Marquette counties, forms one of the prominent areas for spruce-fir in northern Michigan. Spruce-fir in southern Michigan is confined to the few counties at the northern tip of the peninsula and then only along the shores of Lakes Michigan and Huron in low and quite moist situations. Although *Abies balsamea* was abundant in these stands, *Picea glauca* was a very minor component.

Along the east shore of Lake Superior in Ontario, stands of spruce-fir are frequent and mixed spruce-fir-hardwood stands are widespread and contain large proportions of these conifers. These stands are prominent on rocky soils with heavy accumulations of plant litter. Continued natural disturbance appears to be the agent active in maintaining large proportions of conifers in these old hardwoods which otherwise would develop into pure stands. Great expanses of vegetation along the north shore of Lake Huron in Ontario have recently been burned over and spruce-fir is mixed to a considerable extent through the young growth of *Populus* and *Betula papyrifera*. In the Algonquin Park area spruce-fir stands occur most often on sandplains and usually mixed with large amounts of *Populus* and *Pinus strobus*. Scattered specimens of *Abies balsamea* and *Picea glauca* occur in old hardwoods and indicate generally the trends in succession which occur toward the southern limits of spruce-fir in Ontario (Maycock 1956).

METHODS

The methods employed for the collection and treatment of stand composition have been previously described in detail (Cottam & Curtis 1949; Cottam, Curtis & Hale 1953; Cottam & Curtis 1956). In attempting to collect data for many examples of the spruce-fir and spruce-fir-mixed hardwoods community over as extensive an area as the Great Lakes region, the field methods had to be accurate, fairly rapid, and suitable for use by a single operator. Those adopted at the time the study was initiated seemed to be appropriate, and later proved to be most adequate.

SELECTION OF STANDS

At the outset of this phytosociological analysis, little more than general knowledge concerning the variability of forest types, their components, their distribution and other characteristics was available. It was therefore essential to utilize this general knowledge of the community to formulate criteria for the selection of stands, previous to the beginning of field work, in an attempt to establish broad limits, and to prevent subjective selection of samples which may have coincided with any possible preconceived idea of community composition.

The criteria for stand selection were: that they be on upland sites, of at least 15 acres in size, free from unnatural disturbance in the lifetime of the existing components, and with *Picea glauca* present as a member of the tree canopy. In the field these criteria were a definite aid in selecting samples but some judgment was necessary in the final decision. The presence of *Picea glauca* was decided upon as the important boreal indicator to eliminate the study of those stands to the south of the limits of this species, in which *Abies balsamea* is important in the understories and only rarely penetrates the canopy. However, within the range of *Picea glauca*, in a few situations where it was absent and *Abies balsamea* was the dominant boreal constituent, such stands were chosen, provided they satisfied the other criteria. The latter situations were quite rare and although *Picea glauca* may not always have influentially participated in the dominant category it was usually present in the stand, even if sparsely so.

Since spruce-fir vegetation is so markedly and regularly affected by catastrophes of many descriptions and because the community components are not usually long-lived, few of the stands studied could be classified in the virgin state. Stands markedly damaged or opened, either naturally or artificially, were definitely avoided, however.

While size was not a difficult factor to apply rigidly, the determination of the boundaries of the homogeneous stand was to the contrary. Every effort was exerted while sampling to remain on uniform topography, and as a result, any such departures or areas of marked disturbance were avoided to the extent of 50 ft of clearance.

Many of the stands were located using information provided by many helpful persons, but the majority were discovered by the senior author while en route. Certain stands which had previously been sampled in the northern conifer-hardwood study in northern Wisconsin (Brown & Curtis 1952) and which suited the present criteria were incorporated with those recently investigated.

FIELD METHODS

Field work was started in the summer of 1954 and was continued during 1955 and 1956. In the fall of 1956, quantitative data had been collected for a total of 110 stands (Fig. 1), representing a random selection, without prejudice as to specific boreal or boreal-hardwood types, in the Great Lakes area.

For those stands recently sampled, the quarter method (Cottam & Curtis 1956) was utilized while those stands investigated during the northern conifer-hardwood studies were surveyed by means of the random pairs method or some slight modification of it (Cottam & Curtis 1949). A size of 4 in. d.b.h. (diameter, breast height) was chosen as the lower limit for trees. The lower limit for saplings was 1 in. and seedlings were those woody stems up to 1 in. in diameter. These definitions were of considerable significance and greatly affected the value of data obtained. Certain shrub species satisfied the criteria for saplings, but only those species which had the capabilities of attaining tree size, and which had been sampled or observed as trees, were so recorded. Thus *Amelanchier* spp., *Acer spicatum*, *Acer pensylvanicum* and *Alnus rugosa* were recorded as trees and saplings, while species such as *Cornus* spp. and *Viburnum* spp. were recorded only for occurrence in quadrats although often their shoots were of sapling size. The former group of plants mentioned were also of considerable importance in the shrub layer and their frequencies were also recorded.

Lower limits for trees, as well as various methods which sample cover, are unsuitable for censusing in spruce-fir vegetation because of the resulting high representation of *Abies balsamea* which is often very abundant as sapling individuals in the understory. As members of this species age, they become less tolerant and frequently smaller-sized individuals are dying, dead or in a very unhealthy state in dense stands. Over representations, largely the result of these abundant, but far from influential individuals, with respect to their effects on the environment, accordingly reduce the value of the data obtained in formulating interpretations. The method used and the size limits selected appeared to compensate for both of these difficulties.

Stands which from the road appeared suitable, were initially surveyed to determine whether the selection criteria were satisfied, to judge their general condition and extent, and to investigate the presence of disturbance. The distribution of the major dominants was generally observed for homogeneity.

The general sampling procedure was as follows. A starting point was selected at random and with a compass a direction of travel was decided upon. A distance of 30 yards was paced off and a survey point established. After laying a 1 m square quadrat around the point, the presence of all herbs, shrubs and tree seedlings was recorded. Using the compass line as a bisect, the area around the point was divided into 4 imaginary quadrants, and within each, the species and size of each tree nearest to the point, as well as its distance from the point, was determined. Size was measured as the basal area in inches at a point 4.5 ft above the ground. The species of the 4 saplings nearest to the point in each quadrant as well as their distances from the point were also recorded. Then another 30 yds were similarly paced off and the procedure repeated. In general, 40 points per stand were taken, but in smaller or irregular stands often

only 30 were established. At every survey point, trees and saplings were recorded but quadrats were put down only at every other point. Thus in general a sample of 160 trees, 160 saplings and 20 quadrats for shrub, herb and tree seedling frequencies were collected. During these operations a running list of all plant species present was compiled.

Three soil pits, randomly located, were dug and in each the depth of the A₀, A₁ and A₂ horizons were measured. A sample of the A₁ was collected at each pit and the three were pooled for subsequent analysis.

Species of plants not identifiable in the field were collected, appropriately tagged, and later determined. A representative collection of plants was made and specimens are contained in the senior writer's private herbarium as well as in the University of Wisconsin Herbarium. The authority on species nomenclature followed throughout was Gray's Manual of Botany, 8th ed. (Fernald 1950).

The field data, filed in the Plant Ecology Laboratory of the University of Wisconsin are available for critical examination and any additional related studies.

QUANTITATIVE PROCEDURES AND LABORATORY METHODS

Data recorded in the field were tabulated and placed on various summation sheets. Separate forms were prepared for tree information, and for shrub and herb data. Measures of number, size and distribution for each tree species were determined from the data obtained by the quarter method, for each stand individually. The total basal area or dominance was totalled for each species. The points of occurrence as well as the total number of trees of each species (density) were determined. Relative density and relative dominance were calculated by the usual procedure but relative frequency, as percentage sum of frequency (Curtis & McIntosh 1950), rather than the usual simple frequency. Thus relative frequency was the total points of occurrence for each tree species, divided by the total points of occurrence for all species, expressed as a percent. Relative frequency, relative density, and relative dominance were summed to result in a single index or importance value (Curtis & McIntosh 1950). The importance values for all tree species in a stand sum to a constant total of 300. Continued use of the importance index in forest ecological research has supported the contention that it is a better indicator of the relative ecological importance of individual species, than any one of its components (Cain *et al.* 1956). It permits a comparison of the values for any species in different stands upon an equal basis.

The relative densities of saplings and the frequencies for herbs and shrubs were also obtained for each stand. Percent presence or constancy and average percent frequency for all species were finally determined when the data for all stands were assembled.

Homogeneity was among the important criteria used for the selection of stands for study. This was arbitrarily determined in the field by observing the

distributions of major dominants and uniformity of topography. Since no quantitative indications of homogeneity were available previous to sampling, a statistical test was applied to the data, to assure the comparison of stands uniform in this respect. The Chi Square Test (Snedecor 1946) was performed, utilizing the four segments of tree data obtained from sequential sets of 10 sampling points each, as sample groupings in each stand. The test permits a determination of significant deviation of the major tree species in any sample, from expected occurrences on the basis of uniform distribution. At least 5 individuals per theoretical sample are required in the test, and only those species represented by at least 20 individuals, were therefore employed. The application of this test indicated that in none of the 103 stands for which there was complete tree data, did the important species differ significantly from a homogeneous distribution.

Soil acidity and water-retaining capacity were determined on air-dried samples, previously crushed with a mortar and pestle and passed through a 2 mm screen. Acidity was measured by the glass electrode potentiometer. Water-retaining capacity was determined by filling Hilgard soil cups (brass 2 in. diameter, 7/8 in. high) with soil, levelling and then permitting samples to become fully saturated in trays of distilled water. Samples were subsequently weighed, then dried in an oven at 105°C for 72 hours or more, and finally weighed to a constant weight. Water-retaining capacity was calculated by expressing the total wet weight less the total dry weight as a percentage of the total dry weight less the weight of the cup. Soil samples were prepared for mineral analysis of calcium, potassium, phosphorus, nitrate, magnesium and ammonium, by grinding in a Wiley mill until the particles passed through a 2 mm screen. The methods for these nutrient determinations were those in use at the Wisconsin State Soils Laboratory, and concentrations were expressed as pounds per acre for the measured depth and weight of the particular horizon sampled. Such analyses were based solely on the A₁ layer, as collected in the field, often a difficult procedure due to the minute amounts sometimes available. Samples of the humus layer in 10 stands chosen at random, were analyzed for a comparison.

When all floristic and environmental data were assembled, Post-Index sheets, bearing a complete summary of all data, were prepared for each stand. These, folded and placed in overlapping positions in special files, with the columns of figures exposed, provided a very suitable arrangement for the summarizing, filing and processing of the large quantities of data accumulated, and are available for inspection in the Plant Ecology Laboratory, University of Wisconsin.

ORDINATION TECHNIQUES AND RESULTS

TREATMENT OF DATA

The quantitative phytosociological procedures employed in this attempt to solve some of the complex

problems of the upland forest vegetation of the northern Great Lakes area, while they form a reliable basis for ecological interpretations, are characterized by various disadvantages. The first is due to the large number of stands sampled and the resulting large amounts of data to be processed. A total of 110 stands with an average of 13 trees and 54 shrubs and herbs per stand, a total of 440 different vascular species in all, demanded much compilation and made abundant calculations necessary. Any single step needed to be repeated 110 times. The second disadvantage was an outcome of this processing: the loss of individual stand detail by summarizing. This is unfortunately a necessary complication, inherent in attempts to discover community structure and the interrelations of component species. This detail is by no means completely obscured, however, since it figures importantly in subsequent autecological investigations made possible by the knowledge of broader community aspects.

The general pattern of plant sociological procedures is based upon the assumption that each species in nature possesses a characteristic amplitude of tolerance, and is therefore permitted to occupy a specific range of the gradational series of environment available. Vegetation is the resultant of a multitude of associated species, each possessing specific amplitudes of tolerance. In the treatment of vegetation, if all species involved are characterized by similar tolerances and no overlapping or integration of tolerance amplitudes occurs with species considered components of other vegetational types, then a separation of distinct associational units would appear to be justified. Conversely, if no discontinuities between the ecological amplitudes of groups of species are apparent and a continuous overlapping series is apparently related to environmental conditions, universally assumed to be continuous, then such tendencies must be reflected in our methods of describing and characterizing vegetation. If such is the situation and we attempt to superimpose boundaries or a false distinctness, our further efforts will represent but partialities, regardless of how thorough and contributing they may be.

Therefore the necessary approach involves a delimitation of these amplitudes of tolerance and attempts to discover the resulting patterns of their relationships to each other. A technique is required for the objective positioning of stands in some logical order, so that quantitative relationships of the component species form reasonable patterns in accordance with this ordering of stands.

When the tabulation of all stand data was completed, a total of 33 species which regularly attain tree size, and another 9 species which were occasionally encountered as trees in the field, but most commonly occurred as saplings, was indicated. Before other treatments were attempted, a list of the regularly occurring trees was compiled and data indicative of importance in the community were incorporated. This information, provided in Table 1, indicates that of all the tree species only *Abies balsamea*, *Acer rubrum*, *Acer saccharum*, *Betula lutea*, *Betula papyrifera*,

Fagus grandifolia, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Pinus resinosa*, *Pinus strobus*, *Populus grandidentata*, *Populus tremuloides*, *Quercus rubra*, *Thuja occidentalis*, *Tsuga canadensis* and *Ulmus americana* attained significant importance in any single stand. Of this group of 17 species only 7, *Abies balsamea*, *Acer saccharum*, *Picea glauca*, *Pinus strobus*, *Populus tremuloides*, *Thuja occidentalis* and *Tsuga canadensis*, were the leading dominants in at least 5% of the 110 stands. This situation may be dependent somewhat upon the choice of stands, but because an attempt was made to select a wide variety of types and to provide adequate geographical coverage, a fairly random sample resulted.

TABLE 1. List of majority of tree species observed in 110 upland forest stands containing white spruce and/or balsam in the Northern Great Lakes Region with data indicating the relative importance of each.

Species	Stands (Leading Dominant)	Stands Occur. (Presence)	Stands Occur. (I.V.)	Maximum Import. Value
<i>Abies balsamea</i>	35	103	102	234.1
<i>Acer rubrum</i>	—	89	52	69.0
<i>Acer saccharum</i>	8	60	44	135.4
<i>Betula lutea</i>	4	43	36	108.2
<i>Betula papyrifera</i>	4	89	80	140.4
<i>Fagus grandifolia</i>	1	4	4	124.7
<i>Fraxinus americana</i>	—	14	4	26.5
<i>Fraxinus nigra</i>	—	48	22	32.8
<i>Larix laricina</i>	—	13	8	15.9
<i>Ostrya virginiana</i>	—	26	10	14.0
<i>Picea glauca</i>	19	100	99	175.7
<i>Picea mariana</i>	—	29	26	99.0
<i>Pinus banksiana</i>	2	13	13	181.1
<i>Pinus resinosa</i>	2	36	31	166.6
<i>Pinus strobus</i>	11	66	52	180.8
<i>Populus balsamifera</i>	—	24	21	32.8
<i>Populus grandidentata</i>	—	28	19	75.8
<i>Populus tremuloides</i>	5	71	64	256.2
<i>Prunus pensylvanica</i>	—	40	6	5.8
<i>Prunus serotina</i>	—	30	8	18.3
<i>Pyrus americana</i>	—	51	13	24.7
<i>Quercus alba</i>	—	4	2	8.3
<i>Quercus ellipsoidalis</i>	1	5	4	54.7
<i>Quercus macrocarpa</i>	—	5	3	6.9
<i>Quercus rubra</i>	1	37	18	83.6
<i>Thuja occidentalis</i>	11	65	60	174.6
<i>Tilia americana</i>	—	26	17	35.1
<i>Tsuga canadensis</i>	5	37	32	223.0
<i>Ulmus americana</i>	1	32	19	113.7

Few of the minor species were ever important in any stand, but all have comparatively high percent presence values: *Acer rubrum*, *Fraxinus nigra*, *Ostrya virginiana*, *Populus balsamifera*, *Populus grandidentata*, *Prunus pensylvanica*, *Prunus serotina*, *Pyrus americana* and *Tilia americana*. A few species had high percent presence and were rarely leading dominants: *Betula lutea*, *Betula papyrifera*, *Pinus banksiana*, *Pinus resinosa*, *Quercus rubra* and *Ulmus americana*. *Fagus grandifolia* and *Quercus ellipsoidalis* are representative of those tree species which had a low percent presence and yet acted as leading dominants.

In the literature, a mesophytic forest of *Acer saccharum*, *Betula lutea*, *Tsuga canadensis*, and perhaps *Fagus grandifolia* and *Tilia americana* is favored for the position of terminal or climax forest in the southern portion of the study area now considered. Toward the northern sections of the Great Lakes region a terminal forest of *Picea glauca* and *Abies balsamea* has been postulated. These ideas suggested the possibility of a separation of all stands into two principal types or associations and the tree data for stands were carefully examined with this in mind.

Certain stands could without difficulty be placed in one or the other of the categories mentioned but as these clear cut cases diminished a greater difficulty was encountered in classifying stands because of admixtures of species considered decisive in placing stands in both associations. In these cases some other basis than the relative proportions of tree species was required to justify their placement in either association. When only stands dominated by any one of the 4 major species were chosen and arranged in order of decreasing sum of importance values for *Picea glauca* and *Abies balsamea* in one direction, and decreasing sum of importance values for *Acer saccharum* and *Betula lutea* in the opposite direction, a gradational series from almost pure *Picea glauca* and *Abies balsamea* to almost pure *Acer saccharum* and *Betula lutea* or other associated hardwood species, was obtained. Attempts to sort the 67 stands of this series into a *Picea-Abies* or *Acer-Betula* association were accompanied by considerable subjective judgment. Any two experienced ecologists would have undoubtedly favored conflicting separations. Not only the relative amounts of any of the 4 species used in the ordering created difficulty, but the high importance values of many other species was also a contributing factor, adding further to the confusion. The unsuitability of such a treatment to classify even broadly these 67 stands into associational units, to say nothing of the other 43 stands dominated variously by a large group of other species, with these same species present as members of lesser importance, was clearly evident.

The possibility of a polyclimax situation, with types frequently dominated by a few major dominants in somewhat the same sequence of importance, was then examined. Tree species were placed in order of leading dominants based on the importance values in each stand, and the resulting arrangements were considered. *Abies balsamea* was the leading dominant in 35 stands, *Picea glauca* in 19, *Thuja occidentalis* in 11, *Pinus strobus* in 11, *Acer saccharum* in 8, *Tsuga canadensis* in 5 and *Betula lutea* in 4. The leading dominants in the remaining 17 stands are indicated in Table 1.

If types are recognized on the basis of the leading dominant, 15 would need to be established. Forty-eight arrangements of the first 2 leading dominants, 82 of the first 3, 99 of the first 4 and 109 of the first 5, were determined. Thus of the 110 stands, only a single pair was discovered to have the same arrange-

ment of the 5 most important tree species. Although this method of classifying on the basis of leading dominants is objective as now considered, unless an unwieldy number of types is recognized, subjectivity will predominate in the grouping of stands into categories. Again, ecologists would be of widely differing opinions in determining the critical level of importance for the establishment of such categories. While this method may have offered a technique for a tentative classification of stands, it did not permit the manipulations necessary to bring to light, either the interrelations of the tree species themselves, or their effects on understory associates. In any such treatments that may have been attempted on the basis of such a classification, subjective judgment would have entered into every operation and the indiscriminate lumping of quantitative data would have obscured species relationships.

Curtis & McIntosh (1951), in the upland deciduous forests of southern Wisconsin, and Brown & Curtis (1952), in the upland conifer-deciduous forests of the northern parts of the state, succeeded in obtaining meaningful arrangements for the large numbers of stands sampled by the use of objectively derived indices, which permitted a graphical presentation of species interrelationships. These in turn were related to certain environmental factors. Their compositional indices were calculated on the basis of the statistical occurrences of the major tree species involved in the communities considered. The arrangements of stands obtained by these values, furthermore, were meaningful in terms of the successional tendencies which had been tentatively agreed upon for these areas, with the climax adaptational value representing the ability of any particular tree species to survive and reproduce successfully in the terminal forest complexes considered. Since many of the tree species encountered in the present study were common to the areas of these workers, their method was considered.

In the Lakes region, in the upland boreal and boreal conifer-hardwood forests, several successional trends were evident. The various species of *Populus* and *Betula papyrifera* as well as *Pinus banksiana*, *P. resinosa* and *P. strobus* are the important species in pioneer habitats of low moisture and abundant light. In situations of somewhat excessive moisture and poor light conditions *Thuja occidentalis*, *Larix laricina*, *Picea mariana* predominate. Forests composed of *Abies balsamea* and *Picea glauca* were frequently noted in both of these environmental situations as well as on mesic sites of optimum light and moisture conditions and mature soils, where such hardwood species as *Acer saccharum*, *Betula lutea*, *Fagus grandifolia*, also attain a high level of importance. Stands composed of mixtures of these hardwood species with *Picea glauca* and *Abies balsamea* in almost any possible combination, also characterized the forests of mesic sites. The great variety of stand compositions resulting from these admixtures of species coupled with the complex three-sided distributional

pattern, further complicated by series of intermediate stages, tended to obscure successional relationships.

The data for tree reproduction seemed to indicate a trend toward terminal *Acer saccharum* forests, in the absence of disturbances, if such circumstances have meaning in the Lakes region, but on the whole the successional patterns were far from the relative clarity presented in the phytosociological studies in Wisconsin. Also, since the question of climax in the region has been long and vigorously disputed, and the results of the study were expected to clarify this situation somewhat, it appeared unwise to employ these poorly defined successional tendencies as a basis for stand ordination. In short, no apparently meaningful linear gradient based on tree relationships could be deduced, because the opposite ends prerequisite to its establishment were not discernible. In fact, the examination of tree relationships indicated most species possessed a broad range of tolerance and the advisability of employing just tree species in determining existing patterns was finally questioned. This led ultimately to the trial of some important environmental factor as a basis for stand ordination. The moisture conditions of site appeared to be the least complex and most useful of those available.

MOISTURE GRADIENT ORDINATION ARRANGEMENT OF STANDS

In the course of the field work various environmental characteristics such as topography, soil conditions, light penetration, drainage, atmospheric and edaphic moisture conditions were carefully noted in addition to the specific environmental investigations which have already been mentioned. Differences in floristic composition seemed generally to correspond with changes in these environmental factors and appeared most notably evident, the greater the contrast in moisture conditions. The species complement most frequently associated with coarse-textured, well-drained, sandy soils in partially open situations, was markedly distinct from the group of species characteristic of the poorly drained clays of organic soils in densely shaded habitats. Again, the composition of stands on mesic sites, which can be considered intermediate between these extremes, also differed markedly from those stands on the dry and wet sites. As data for many stands in a wide variety of environmental situations were accumulated, it became increasingly evident that, in spite of these differences between stands on the 3 extreme sites, they were not so markedly different when considered with groups of stands on sites intermediate between the extremes. In short, a gradational series occurred from the one extreme to the other, and the possibility of sharp differentiation on the basis of any single factor was impossible. In an attempt to portray this series, if it so existed, an arbitrary division of moisture classes seemed reasonable, in order to compare species interactions with gradual changes in water relations. On the other hand, if discrete associations were in existence but unobserved by the investigators, it was

considered that this same treatment would be successful in bringing such evidence to bear.

A tentative separation of 5 moisture segments from dry to mesic to wet, with intermediate classes of dry-mesic and wet-mesic was established. Actual moisture conditions were most important in this regard, but the apparent effects of moisture on other factors was also considered. Such factors as soil type, soil texture, depth of soil, drainage pattern, topography, slope, incorporated organic matter, depth of water table, presence of glei, and the broad physiognomic aspects of vegetation, proved of value in this respect. Naturally, great variability was characteristic of many of these factors, even in stands assigned to the same moisture grouping. Again, the specific effects of any of these listed factors on the moisture conditions of the site, are not fully understood by the writers.

TABLE 2. Percent presence and average importance values for trees by moisture segments—moisture gradient data for 103 stands.

Species	PERCENT PRESENCE					AV. IMPORTANCE VALUE				
	D	DM	M	WM	W	D	DM	M	WM	W
<i>Abies balsamea</i>	100	100	100	100	53	57	67	61	95	95
<i>Acer negundo</i>	—	—	7	—	—	—	—	—	—	—
<i>Acer pensylvanicum</i>	18	—	10	13	—	—	—	—	—	—
<i>Acer rubrum</i>	100	95	86	87	64	15	11	12	3	3
<i>Acer saccharum</i>	27	50	67	78	21	5	32	21	—	—
<i>Acer spicatum</i>	36	70	88	96	71	—	—	—	—	—
<i>Aitus rugosa</i>	9	20	14	35	79	—	—	—	—	—
<i>Amelanchier</i> spp.	91	75	69	57	21	—	—	—	—	—
<i>Betula lutea</i>	27	15	55	44	29	22	19	8	—	—
<i>Betula papyrifera</i>	100	95	83	83	20	30	20	18	16	16
<i>Carpinus caroliniana</i>	—	5	2	9	—	—	—	—	—	—
<i>Carya cordiformis</i>	—	5	—	4	—	—	—	—	—	—
<i>Crataegus</i> spp.	—	20	12	4	7	—	—	—	—	—
<i>Fagus grandifolia</i>	—	—	10	—	—	—	5	—	—	—
<i>Fraxinus americana</i>	—	10	12	30	7	—	—	3	—	—
<i>Fraxinus nigra</i>	—	40	41	65	71	1	1	3	6	6
<i>Fraxinus pennsylvanicum</i>	—	—	2	—	7	—	—	—	—	—
<i>Larix laricina</i>	27	5	2	17	36	—	—	1	—	—
<i>Ostrya virginiana</i>	—	25	36	30	—	—	1	1	—	—
<i>Picea glauca</i>	100	100	93	96	100	68	46	35	40	20
<i>Picea mariana</i>	64	20	7	26	64	17	3	1	2	18
<i>Pinus banksiana</i>	27	25	7	4	7	22	8	1	1	9
<i>Pinus resinosa</i>	91	55	26	26	14	21	33	2	3	2
<i>Pinus strobus</i>	100	70	64	70	21	78	39	24	10	1
<i>Populus tremuloides</i>	9	20	19	30	43	—	2	2	5	3
<i>Populus grandidentata</i>	55	60	17	17	7	4	7	2	1	2
<i>Populus tremuloides</i>	82	85	55	78	71	14	44	19	31	18
<i>Prunus nigra</i>	—	5	2	—	—	—	—	—	—	—
<i>Prunus pensylvanica</i>	55	60	38	26	—	—	—	—	—	—
<i>Prunus serotina</i>	55	45	21	26	7	1	1	—	—	—
<i>Prunus virginiana</i>	27	80	43	70	29	—	—	—	—	—
<i>Pyrus americana</i>	27	35	62	48	43	—	1	1	—	—
<i>Quercus alba</i>	9	5	—	9	—	—	—	1	—	—
<i>Quercus ellipsoidalis</i>	18	10	—	4	—	—	—	3	—	—
<i>Quercus macrocarpa</i>	—	10	5	4	—	—	—	—	—	—
<i>Quercus rubra</i>	36	50	43	26	14	1	7	1	1	—
<i>Salix</i> sp.	—	5	2	4	—	—	—	—	—	—
<i>Thuja occidentalis</i>	18	30	76	78	86	—	125	38	87	—
<i>Tilia americana</i>	—	25	33	30	—	—	4	3	—	—
<i>Tsuga canadensis</i>	18	15	52	48	7	—	121	21	—	—
<i>Ulmus americana</i>	—	50	26	44	14	1	1	2	3	8
<i>Ulmus rubra</i>	—	5	5	—	—	—	—	—	—	—

TABLE 3. Percent presence and average percent frequency for herbs and shrubs in various moisture segments—moisture gradient data for 102 stands.

Species	PERCENT PRESENCE						AVERAGE % FREQUENCY					
	D	DM	M	WM	W	D	DM	M	WM	W	D	DM
<i>Achillea millefolium</i>	46	20	17	17	—	1	2	—	—	—	—	—
<i>Aclaea pachypoda</i>	—	15	19	17	7	—	1	—	—	—	—	—
<i>Adeaa rubra</i>	—	50	57	61	43	—	2	2	2	2	—	—
<i>Adenocodon bicolor</i>	—	—	5	—	—	—	—	—	—	—	—	—
<i>Adiantum pedatum</i>	—	—	2	13	—	—	—	—	—	—	—	—
<i>Agrimonia gryposepala</i>	—	15	7	13	14	—	—	—	—	—	—	—
<i>Agrostis alba</i>	—	—	5	4	—	—	—	—	—	—	—	—
<i>Allium tricoccum</i>	—	—	2	4	—	—	—	—	—	—	—	—
<i>Alnus rugosa</i>	—	15	26	48	86	—	—	—	7	—	—	—
<i>Amelanchier sp.</i>	—	—	5	—	—	—	—	1	—	—	—	—
<i>Amphicarpa bracteata</i>	—	10	5	9	—	—	5	1	—	—	—	—
<i>Anaphalis margaritacea</i>	73	20	17	26	14	2	—	—	—	—	—	—
<i>Arenaria canadensis</i>	9	10	7	4	—	—	—	—	—	—	—	—
<i>Anemone cylindrica</i>	—	15	2	—	—	—	—	—	—	—	—	—
<i>Anemone quinquefolia</i>	36	70	52	48	21	8	25	3	5	4	—	—
<i>Anemone virginiana</i>	—	5	5	—	—	—	—	—	—	—	—	—
<i>Anemone thalictroides</i>	—	—	—	4	—	—	—	—	—	—	—	—
<i>Antennaria sp.</i>	46	25	7	4	—	1	—	—	—	—	—	—
<i>Apocynum androsaemifolium</i>	82	65	41	30	7	4	5	1	1	—	—	—
<i>Aquilegia canadensis</i>	18	55	21	13	—	—	2	2	—	—	—	—
<i>Aralia hispida</i>	—	—	2	—	—	—	—	—	—	—	—	—
<i>Aralia nudicaulis</i>	100	95	95	96	93	35	30	30	19	26	—	—
<i>Aralia racemosa</i>	—	5	17	22	14	—	—	1	1	—	—	—
<i>Arctodaphne los uss-ursi</i>	9	—	—	—	—	—	—	—	—	—	—	—
<i>Arenaria lateriflora</i>	—	—	2	—	—	—	—	—	—	—	—	—
<i>Arisaema triphyllum</i>	—	5	21	39	36	—	1	2	4	—	—	—
<i>Asarum canadense</i>	—	20	19	26	7	—	4	3	2	—	—	—
<i>Aster ciliolatus</i>	9	25	5	35	29	—	2	1	1	3	—	—
<i>Aster lateriflorus</i>	—	30	21	48	29	—	1	2	5	2	—	—
<i>Aster macrophyllus</i>	91	100	79	78	57	33	66	42	41	25	—	—
<i>Aster nova-angliae</i>	9	5	—	29	—	—	—	1	—	—	—	—
<i>Aster puniceus</i>	—	—	4	—	—	—	—	—	—	—	—	—
<i>Aster sagittifolius</i>	—	20	14	9	—	2	1	1	—	—	—	—
<i>Aster umbellatus</i>	36	20	10	35	14	1	—	1	1	—	—	—
<i>Athyrium felix-femina</i>	—	55	64	70	43	—	1	3	4	7	—	—
<i>Athyrium thelypteroides</i>	—	—	—	4	7	—	—	—	1	—	—	—
<i>Botrychium matricariaceum</i>	9	—	5	—	—	—	—	—	—	—	—	—
<i>Botrychium multifidum</i>	9	—	2	4	—	—	—	—	—	—	—	—
<i>Botrychium virginianum</i>	—	35	45	48	71	—	2	2	4	4	—	—
<i>Brachelytrum erectum</i>	—	50	60	57	29	3	5	11	3	—	—	—
<i>Bromus ciliatus</i>	—	5	—	14	—	2	—	3	—	—	—	—
<i>Bromus purgans</i>	—	5	3	4	—	—	2	—	—	—	—	—
<i>Calamagrostis canadensis</i>	—	—	—	9	—	—	—	1	—	—	—	—
<i>Calla palustris</i>	—	—	—	21	—	—	—	—	—	—	—	—
<i>Caltha palustris</i>	—	—	—	4	50	—	—	2	—	—	—	—
<i>Campanula rotundifolia</i>	9	—	2	—	—	—	—	—	—	—	—	—
<i>Carex arctata</i>	—	25	45	44	43	5	8	5	7	—	—	—
<i>Carex aura</i>	—	—	2	—	—	—	—	—	—	—	—	—
<i>Carex brunneonervis</i>	—	—	7	4	14	—	—	—	—	—	—	—
<i>Carex communis</i>	—	5	2	—	—	—	—	—	—	—	—	—
<i>Carex disperma</i>	—	—	—	57	—	—	—	16	—	—	—	—
<i>Carex eburnea</i>	—	—	5	9	21	—	2	6	—	—	—	—
<i>Carex indumentacea</i>	—	20	38	26	71	—	1	2	18	—	—	—
<i>Carex leptalea</i>	—	—	—	—	57	—	—	14	—	—	—	—
<i>Carex pedunculata</i>	9	45	57	57	71	—	16	15	18	18	—	—
<i>Carex pensylvanica</i>	27	55	41	30	43	3	14	9	4	5	—	—
<i>Carex projecta</i>	—	5	12	17	14	—	1	2	1	—	—	—
<i>Carex stipata</i>	—	—	—	—	21	—	—	—	—	—	—	—
<i>Carex triplandra</i>	—	—	—	9	43	—	—	125	—	—	—	—
<i>Caulophyllum thalictroides</i>	—	5	10	9	—	—	—	—	—	—	—	—
<i>Celastrus scandens</i>	—	10	12	4	—	—	—	—	—	—	—	—
<i>Ceratium sp.</i>	—	—	7	—	—	—	—	—	—	—	—	—
<i>Chimaphila umbellata</i>	46	40	12	13	7	2	2	1	—	—	—	—
<i>Chrysanthemum leucanthemum</i>	—	36	5	2	—	—	—	—	—	—	—	—
<i>Chrysosplenium americanum</i>	—	—	2	—	—	—	—	—	—	—	—	—
<i>Cicutla maculata</i>	—	—	—	4	14	—	—	—	7	—	—	—
<i>Cinna latifolia</i>	—	—	5	13	29	—	—	—	7	—	—	—
<i>Cirsium alpina</i>	—	20	38	52	64	1	3	6	13	—	—	—
<i>Cirsium arvense</i>	—	—	10	5	4	—	—	—	—	—	—	—

TABLE 3—continued

Species	PERCENT PRESENCE						AVERAGE % FREQUENCY					
	D	DM	M	WM	W	D	DM	M	WM	W	D	DM
<i>Cirsium muticum</i>	—	—	2	—	—	14	—	—	—	—	—	2
<i>Cirsium sp.</i>	9	5	17	4	7	—	—	—	—	—	—	—
<i>Claytonia caroliniana</i>	—	—	5	—	—	—	—	—	—	—	—	—
<i>Clematis virginiana</i>	—	—	10	—	13	—	—	—	—	—	—	1
<i>Clintonia borealis</i>	73	90	93	87	93	17	18	30	25	34	—	—
<i>Comptonia peregrina</i>	36	10	2	—	—	2	—	—	—	—	—	—
<i>Convolvulus spithameus</i>	—	20	2	4	—	—	2	—	—	1	—	—
<i>Coptis groenlandicum</i>	55	40	60	65	86	5	5	10	15	49	—	—
<i>Corallorhiza maculata</i>	9	20	33	4	7	—	—	—	—	—	—	—
<i>Corallorhiza striata</i>	—	5	7	9	14	—	—	—	—	—	—	—
<i>Corallorhiza trifida</i>	—	—	5	22	21	—	—	—	—	—	—	—
<i>Cornus alternifolia</i>	—	40	33	35	—	—	2	3	2	2	—	—
<i>Cornus canadensis</i>	100	95	88	91	93	61	24	24	31	55	—	—
<i>Cornus racemosa</i>	—	15	14	17	14	—	1	1	1	1	—	—
<i>Cornus rugosa</i>	18	50	31	57	36	1	2	3	4	3	—	—
<i>Cornus stolonifera</i>	9	—	5	13	14	—	—	—	—	—	—	—
<i>Corydalis sempervirens</i>	9	5	—	—	—	—	—	—	—	—	—	—
<i>Corylus americana</i>	9	5	—	4	—	—	—	—	—	—	—	—
<i>Corylus cornuta</i>	91	90	83	78	50	23	28	11	10	1	—	—
<i>Cryptotaenia canadensis</i>	—	—	2	—	—	—	—	—	—	—	—	—
<i>Cynoglossum boreale</i>	9	15	5	9	—	1	—	—	—	—	—	—
<i>Cynoglossum officinale</i>	—	5	2	—	—	—	—	—	—	—	—	—
<i>Cypripedium acaule</i>	—	15	10	9	21	—	—	—	—	—	—	—
<i>Cypripedium calceolus</i>	—	—	2	9	21	—	—	—	—	—	—	—
<i>Cystopteris bulbifera</i>	—	—	—	9	—	—	—	—	—	—	—	—
<i>Cystopteris fragilis</i>	—	10	14	17	21	—	1	1	1	1	—	—
<i>Dalibarda repens</i>	46	—	—	—	8	—	—	—	—	—	—	—
<i>Dentaria diphylla</i>	—	—	—	7	—	—	—	—	—	—	—	—
<i>Desmodium glabratum</i>	—	—	2	—	9	—	—	—	—	—	—	1
<i>Dicentra cucullaria</i>	—	—	2	—	—	—	—	—	—	—	—	—
<i>Diervilla lonicera</i>	91	100	64	74	36	24	30	7	11	4	—	—
<i>Dirca palustris</i>	—	15	10	13	—	—	2	1	—	—	—	—
<i>Dryopteris cristata</i>	—	10	12	13	50	—	—	—	—	—	—	—
<i>Dryopteris cristata</i>	9	—	2	4	—	—	—	—	—	—	—	—
<i>Dryopteris marginalis</i>	9	15	31	30	50	—	—	2	1	3	—	—
<i>Dryopteris spinulosa</i>	46	70	88	87	86	—	2	19	16	27	—	—
<i>Epipactis virginiana</i>	—	—	5	—	—	—	—	—	—	—	—	—
<i>Epipactis repens</i>	73	20	5	13	21	4	1	1	1	3	—	—
<i>Epilobium angustifolium</i>	46	25	21	17	29	2	—	—	—	—	—	—
<i>Epilobium glandulosum</i>	—	—	5	13	14	—	—	—	—	—	—	—
<i>Equisetum arvense</i>	9	20	29	57	50	1	2	2	2	2	7	7
<i>Equisetum fluviatile</i>	—	—	—	43	—	—	—	—	—	—	—	—
<i>Equisetum scirpoideum</i>	—	—	5	17	14	—	—	—	—	—	—	—
<i>Equisetum sylvaticum</i>	9	35	36	44	50	—	2	2	3	6	—	—
<i>Erigeron philadelphicus</i>	9	5	2	9	7	—	—	—	—	—	—	—
<i>Erigeron strigosus</i>	46	10	3	—	—	1	—	—	—	—	—	—
<i>Erythronium americanum</i>	—	—	2	—	—	—	—	—	—	—	—	—
<i>Eupatorium maculatum</i>	—	—	—	9	21	—	—	—	—	—	—	—
<i>Fagopyrum sagittatum</i>	—	—	2	4	—	—	—	—	—	—	—	—
<i>Fragaria virginiana</i>	36	75	57	83	50	3</td						

TABLE 3—continued

Species	PERCENT PRESENCE					AVERAGE % FREQUENCY				
	D	DM	M	WM	W	D	DM	M	WM	W
<i>Habenaria orbiculata</i>	9	—	7	99	—	—	—	—	—	—
<i>Habenaria viridis</i>	—	—	5	4	7	—	—	—	—	—
<i>Halenia deflexa</i>	—	10	12	9	21	—	—	1	—	—
<i>Hamamelis virginiana</i>	9	10	—	—	—	—	—	—	—	—
<i>Helianthus sp.</i>	—	10	—	4	—	—	—	1	—	—
<i>Hepatica acutiloba</i>	—	10	—	4	—	—	1	—	—	—
<i>Hepatica americanum</i>	18	75	26	35	7	1	12	6	2	—
<i>Heracleum maximum</i>	—	—	—	13	7	—	—	—	—	—
<i>Heuchera richardsonii</i>	—	—	—	4	—	—	—	—	—	—
<i>Hieracium aurantiacum</i>	55	25	10	22	7	12	2	—	—	—
<i>Hieracium canadense</i>	18	—	—	7	—	—	—	1	—	—
<i>Hieracium pratense</i>	36	—	2	4	—	—	—	1	—	—
<i>Hieracium scabrum</i>	36	15	10	4	—	2	2	—	—	—
<i>Hydrophyllum virginianum</i>	—	—	—	4	—	—	—	—	—	—
<i>Hydrastis canadensis</i>	—	—	—	9	—	—	—	—	—	—
<i>Ilex verticillata</i>	—	10	14	13	21	—	—	—	—	—
<i>Impatiens capensis</i>	—	10	24	21	50	—	1	2	11	—
<i>Iris lacustris</i>	—	—	2	—	7	—	—	—	—	—
<i>Iris versicolor</i>	—	—	—	—	21	—	—	—	—	—
<i>Isopyrum bipteratum</i>	—	—	—	2	—	—	—	—	—	—
<i>Juniperus communis</i>	9	—	—	—	—	—	—	—	—	—
<i>Lactuca canadensis</i>	9	25	12	9	14	—	2	1	1	—
<i>Laportea canadensis</i>	—	—	10	4	7	—	—	—	—	—
<i>Lathyrus ochroleucus</i>	—	40	17	26	14	—	4	1	3	1
<i>Ledum groenlandicum</i>	27	5	—	4	36	—	—	2	—	—
<i>Lilium michiganense</i>	—	5	5	9	—	—	—	—	—	—
<i>Linnæa borealis</i>	91	75	57	74	86	12	9	11	13	37
<i>Listeria cordata</i>	—	—	—	14	—	—	—	1	—	—
<i>Lonicera canadensis</i>	46	80	91	96	86	—	4	9	8	8
<i>Lonicera dioica</i>	—	—	2	4	7	—	—	—	—	—
<i>Lonicera hirsuta</i>	—	65	43	48	21	—	3	2	2	1
<i>Lonicera oblongifolia</i>	—	20	7	4	7	—	1	—	—	—
<i>Lonicera prolifera</i>	15	—	—	—	—	—	—	—	—	—
<i>Lonicera villosa</i>	—	—	—	4	7	—	—	1	—	—
<i>Luzula acuminata</i>	—	25	17	4	36	—	3	1	6	—
<i>Luzula multiflora</i>	—	10	2	—	—	—	—	—	—	—
<i>Lycopodium annotinum</i>	73	25	48	52	36	12	1	3	4	1
<i>Lycopodium clavatum</i>	82	60	36	48	21	21	5	3	1	1
<i>Lycopodium complanatum</i>	64	10	7	9	14	1	—	1	—	—
<i>Lycopodium lucidulum</i>	18	20	48	61	14	1	—	8	9	2
<i>Lycopodium oblongulum</i>	82	70	67	39	21	22	9	7	7	—
<i>Lycopodium triplachyum</i>	36	—	—	—	1	—	—	—	—	—
<i>Lycoporus americanus</i>	—	—	—	9	—	—	—	—	—	—
<i>Lycoporus uniflorus</i>	—	—	5	13	50	—	—	1	5	—
<i>Lysimachia ciliata</i>	—	20	7	—	14	—	—	—	—	—
<i>Lysimachia quadrifolia</i>	—	15	—	—	—	2	—	—	—	—
<i>Lysimachia terrestris</i>	—	—	—	7	—	—	—	—	—	—
<i>Maianthemum canadense</i>	100	100	100	100	66	56	55	46	44	—
<i>Malaxis unifolia</i>	—	—	—	4	—	—	—	—	—	—
<i>Medeola virginiana</i>	—	—	7	4	—	—	—	—	—	—
<i>Melampyrum lineare</i>	91	25	12	22	14	19	—	1	1	—
<i>Mentha arvensis</i>	—	—	—	14	—	—	—	—	—	—
<i>Mertensia paniculata</i>	—	10	14	4	—	—	1	2	1	—
<i>Milium effusum</i>	—	—	7	4	7	—	—	1	—	—
<i>Mitchella repens</i>	18	40	43	35	7	—	8	6	6	—
<i>Mitella diphylla</i>	—	15	10	17	—	—	1	1	2	—
<i>Mitella nuda</i>	—	30	55	78	86	—	4	17	24	49
<i>Moneses uniflora</i>	9	35	19	13	50	—	1	1	2	5
<i>Monotropa hypopithys</i>	9	5	7	—	—	1	—	—	—	—
<i>Monotropa uniflora</i>	27	10	19	9	14	1	—	1	—	—
<i>Nemopanthus mucronata</i>	—	—	—	—	14	—	—	—	—	—
<i>Onclea sensibilis</i>	—	5	7	17	43	—	—	1	—	—
<i>Orchis spectabilis</i>	—	—	—	2	—	—	—	—	—	—
<i>Oryzopsis asperifolia</i>	55	90	57	70	7	8	35	11	16	1
<i>Osmorhiza claytoni</i>	—	35	55	39	14	—	2	4	1	1
<i>Osmorhiza longistylis</i>	—	—	5	7	9	—	—	—	—	—
<i>Osmunda claytoniana</i>	18	35	33	35	21	—	—	—	—	—
<i>Osmunda cinnamomea</i>	18	15	24	30	43	—	—	1	4	—
<i>Osmunda regalis</i>	—	—	—	—	14	—	—	—	—	—
<i>Oxalis montana</i>	9	5	21	44	50	1	—	4	6	20
<i>Panax quinquefolius</i>	—	1	—	—	—	—	—	—	—	—

TABLE 3—continued

Species	PERCENT PRESENCE					AVERAGE % FREQUENCY				
	D	DM	M	WM	W	D	DM	M	WM	W
<i>Panax trifolius</i>	—	—	7	9	—	—	—	—	—	—
<i>Parthenocissus inserta</i>	—	10	—	—	4	—	—	—	—	—
<i>Parthenocissus quinquefolia</i>	—	10	2	—	—	—	—	—	—	—
<i>Pedicularis canadensis</i>	9	5	2	—	—	—	—	—	—	—
<i>Petasites palmatus</i>	—	30	36	44	57	—	6	4	3	7
<i>Phegopteris pratense</i>	9	5	5	9	—	—	—	—	—	—
<i>Plantago major</i>	—	—	5	9	—	—	—	—	—	—
<i>Poa compressa</i>	9	20	14	9	7	—	2	1	1	—
<i>Poa pratensis</i>	—	—	—	—	4	—	—	—	—	—
<i>Podophyllum peltatum</i>	82	55	12	17	29	22	8	2	4	—
<i>Polygonatum pubescens</i>	18	45	29	22	—	—	4	2	5	—
<i>Polygonum ciliinode</i>	9	—	5	—	—	—	—	—	—	—
<i>Polygonum sagittatum</i>	—	—	—	4	7	—	—	—	—	—
<i>Polyodium virginianum</i>	18	5	7	4	—	—	—	—	—	—
<i>Potentilla norvegica</i>	18	—	—	—	—	—	1	—	—	—
<i>Prenanthes alba</i>	9	60	33	30	14	1	2	2	1	—
<i>Prunella vulgaris</i>	9	20	29	35	50	—	—	2	2	—
<i>Prunus nigra</i>	—	5	—	—	—	—	—	—	—	—
<i>Pteridium pensylvanicum</i>	—	5	10	9	—	—	1	—	—	—
<i>Pteridium aquilinum</i>	91	100	69	74	36	78	41	12	13	7
<i>Pterospora andromedea</i>	9	—	—	—	—	—	—	—	—	—
<i>Pyrola asarifolia</i>	27	30	26	35	21	1	7	4	1	—
<i>Pyrola elliptica</i>	55	55	48	35	7	3	2	3	1	1
<i>Pyrola minor</i>	—	—	5	—	—	—	—	—	—	—
<i>Pyrola rotundifolia</i>	18	40	—	9	—	2	2	—	—	—
<i>Pyrola secunda</i>	46	80	52	57	64	1	4	4	3	11
<i>Pyrola virens</i>	9	10	7	4	—	—	—	—	—	—
<i>Ranunculus abortivus</i>	—	5	12	4	14	—	—	2	—	—
<i>Ranunculus acris</i>	—	10	19	9	7	—	—	1	1	3
<i>Ranunculus recurvatus</i>	—	10	7	13	7	—	—	1	1	1
<i>Ranunculus septentrionalis</i>	—	5	2	4	14	—	—	—	—	—
<i>Rhamnus alnifolia</i>	—	—	10	9	21	—	—	—	—	—
<i>Rhus radicans</i>	9	35	10	17	7	—	5	1	1	—
<i>Rhus typhina</i>	—	—	2	—	—	—	—	—	—	—
<i>Ribes americanum</i>	9	—	5	—	—	—	—	—	—	—
<i>Ribes cymosbatum</i>	—	55	31	44	29	—	3	2	1	3
<i>Ribes glandulosum</i>	—	15	7	17	14	—	—	—	—	—
<i>Ribes lacustre</i>	—	—	7	13	7	—	2	—	—	—
<i>Ribes triste</i>	9	20	36	52	57	1	1	2	5	—
<i>Rosa sp.</i>	36	50	33	39	36	3	8	3	4	1
<i>Rubus idaeus</i>	55	70	67	48	50	6	6	3	4	3
<i>Rubus parviflorus</i>	—	15	43	35	14	—	4	18	4	3
<i>Rubus pubescens</i>	82	90	69	83	100	5	27	15	18	54
<i>Rubus (blackberry)</i>	36	45	14	30	7	5	7	2	2	—
<i>Rumex acetosella</i>	18	—	—	4	—	1	—	—	—	—
<i>Salix spp.</i>	55	40	9	35	36	1	1	1	1	1
<i>Sambucus pubens</i>	27	20	38	30	14	1	—	—	—	—
<i>Sanguinaria canadensis</i>	—	10	2	—	—	—	—	—	—	—
<i>Sanicula marilandica</i>	9	55	31	44	7	—	8	6	1	1
<i>Satureja vulgaris</i>	9	15	21	13	—	—	2	2	—	—
<i>Saxifrage pensylvanica</i>	—	—	2	4	21	—	—	—	—	—
<i>Schizachne purpurascens</i>	9	20	7	—	—	1	2	1	—	—
<i>Scutellaria piloselloides</i>	—	—	—	—	—	—	—	36	—	—
<i>Scutellaria lateriflora</i>	—	5	2	4	14	—	—	—	2	—
<i>Senecio aureus</i>	—	5	—	—	9	—	—	—	—	—
<i>Shepherdia canadensis</i>	9	5	2	9	—	—	—	—	—	—
<i>Sium suave</i>	—	—	—	—	14	—	—	—	—	—
<i>Smilacina racemosa</i>	18	40	29	35	—	2	1	1	1	1
<i>Smilacina stellata</i>	9	5	7	—	—	—	—	—	—	5
<i>Smilacina trifolia</i>	—	—	—	—	—	—	—	21	—	—
<i>Smilax ecirrhata</i>	—	25	7	—	—	—	—	—	—	—
<i>Smilax tamnoides</i>	—	10	2	—	—	—	—	—	—	—
<i>Spiranthes romanzoffiana</i>	27	—	—	—	—	—	—	—	—	—
<i>Solidago canadensis</i>	36	10	5	9	—	3	2	1	—	—
<i>Solidago flexicaulis</i>	—	10	10	26	7	—	—	—	—	—
<i>Solidago graminifolia</i>	27	5	—	—	—	—	—	—	—	—
<i>Solidago hispida</i>	9	10	2	—	—	—	—	—		

TABLE 3—continued

Species	PERCENT PRESENCE					AVERAGE % FREQUENCY				
	D	DM	M	WM	W	D	DM	M	WM	W
<i>Solidago</i> sp.	—	10	5	9	—	—	1	—	—	—
<i>Solidago ulmifolia</i>	—	5	2	9	7	—	—	—	—	1
<i>Sphagnum</i> spp.	—	—	—	17	57	—	—	—	—	38
<i>Spiraea alba</i>	46	5	—	4	—	1	—	—	—	—
<i>Streptopus amplexifolius</i>	9	—	2	—	14	—	—	—	—	—
<i>Streptopus roseus</i>	46	90	91	83	87	4	12	21	15	3
<i>Symphoricarpos occidentalis</i>	—	20	7	4	—	—	2	—	—	—
<i>Taraxacum officinale</i>	46	35	29	35	14	1	3	2	2	1
<i>Taxus canadensis</i>	—	15	29	30	29	—	—	10	9	—
<i>Thalictrum dasycarpum</i>	—	—	—	4	7	—	—	—	—	—
<i>Thalictrum dioicum</i>	9	35	19	39	21	—	6	4	3	3
<i>Tiarella cordifolia</i>	9	—	—	4	—	—	—	—	—	—
<i>Trientalis borealis</i>	91	75	95	91	100	39	19	23	23	39
<i>Trifolium hybridum</i>	—	—	2	—	—	—	—	—	—	—
<i>Trifolium pratense</i>	—	20	12	4	—	—	—	—	—	—
<i>Trifolium repens</i>	36	20	14	9	—	—	1	1	—	—
<i>Trillium cernuum</i>	—	30	43	39	57	—	1	—	2	1
<i>Trillium erectum</i>	9	—	—	—	—	—	—	—	—	—
<i>Trillium grandiflorum</i>	9	20	12	9	—	1	3	1	—	—
<i>Triosteum perfoliatum</i>	—	5	—	—	7	—	—	—	—	—
<i>Uvularia grandiflora</i>	—	15	14	13	7	—	1	2	1	—
<i>Uvularia sessilifolia</i>	9	55	41	26	7	2	6	6	3	—
<i>Vaccinium angustifolium</i>	100	65	24	35	50	51	11	1	4	10
<i>Vaccinium myrtillodes</i>	100	55	17	39	50	20	7	—	3	10
<i>Vaccinium oxycoccus</i>	—	—	—	—	7	—	—	—	—	—
<i>Veronica scutellata</i>	—	2	—	7	—	—	—	—	—	—
<i>Veronica serpyllifolia</i>	—	—	5	—	—	—	—	—	—	—
<i>Viburnum acerifolium</i>	9	20	5	—	—	1	1	—	—	—
<i>Viburnum cassinoides</i>	36	—	7	9	7	1	—	—	—	—
<i>Viburnum lentago</i>	—	5	5	4	—	—	—	—	—	—
<i>Viburnum rafinesqueianum</i>	—	35	19	13	7	—	3	2	—	—
<i>Viburnum trilobum</i>	9	25	10	13	7	—	—	1	—	—
<i>Vicia americana</i>	—	15	12	13	7	—	1	—	—	—
<i>Viola adunca</i>	—	10	—	—	—	—	—	—	—	—
<i>Viola canadensis</i>	—	7	4	7	—	—	1	—	5	—
<i>Viola conspersa</i>	9	65	31	48	7	1	5	3	6	1
<i>Viola cucullata</i>	—	20	17	4	7	—	1	2	—	—
<i>Viola incognita</i>	36	65	76	87	50	2	9	22	26	12
<i>Viola nephrophylla</i>	18	—	—	—	2	—	—	—	—	—
<i>Viola pallens</i>	—	—	5	22	71	—	—	4	31	—
<i>Viola papilionacea</i>	27	5	2	—	3	—	—	—	—	—
<i>Viola pubescens</i>	—	60	48	22	14	—	1	2	2	2
<i>Viola renifolia</i>	18	30	57	52	36	—	1	5	7	2
<i>Viola septentrionalis</i>	—	—	2	—	—	—	—	2	—	—
<i>Walsteinia fragarioides</i>	18	45	2	9	14	18	23	—	4	1
<i>Woodsia ilvensis</i>	—	5	2	4	—	—	—	—	—	—

Further to complicate the situation, moisture conditions varied with weather and season, but generally the mesic sites were least affected by such fluctuations. In the field a stand had been classified after a preliminary survey and an examination of these factors, before any quantitative floristic measurements were taken. In general, the range in moisture conditions was not difficult to establish. The dry, mesic, and wet situations presented the least trouble. Where moisture conditions were not clearly evident, the discrepancies could only have influenced moisture position by one segment.

ACTION OF PLANT SPECIES

The distribution of the 110 stands in the 5 moisture segments was as follows; dry 11, dry-mesic 20, mesic 42, wet-mesic 23, and wet 14. A sufficient

number of stands are included in each segment to prevent bias and to result in meaningful averages.

Presence values for trees, shrubs and herbs were averaged for each moisture segment for the 110 stands. Importance values for trees and frequency values for herbs and shrubs were similarly averaged for 102 stands for which complete quantitative data were available. These percent presence and average importance values for tree species, in each moisture segment appear in Table 2, while the percent presence and average percent frequency values for herbs and shrubs in sequential moisture segments are presented in Table 3.

The set of values for any single species across the 5 moisture segments, shows that a tendency to attain optimum importance in a particular category or in adjacent segments, exists. This phenomenon is exhibited by almost every plant species for which sufficient data are available. It is also evident that the trends displayed by presence averages are usually corroborated by the frequency averages in this respect. Certain species may be confined to a narrow range of moisture conditions, whereas others may demonstrate a broad amplitude of tolerance and appear to reach optima external to the conditions of moisture defining the limits of this study. In this respect it should be clarified that "dry" and "wet" segments of the moisture gradient are not the driest and wettest conditions possible for forest growth in the Lakes region. These extremes of moisture are within those determining the environmental limits of *Picea glauca*. This species was not seen in stands of sufficient extent to be sampled within the criterion of stand size decided upon, in extremely dry and extremely wet situations, although single specimens occasionally occurred in such situations.

If the series of values for each species is carefully examined it is readily perceived that a majority might be separately categorized on the basis of ability to attain optima in specific moisture segments. If, in selecting these moisture indicating species, one were to be restrictive and select only those with prominent highest values or "peaks" in any one moisture segment, groups of species, indicative of moisture conditions of site, would be separated and might prove of value in the future determination of moisture conditions in additional stands.

As an additional aid to understanding and interpreting the relationships of species to the moisture gradient, various quantitative aspects for selected groups of species have been graphed along the series. In general and for a majority of the species, the distribution of values resembles more or less a normal or binomial curve. It should be understood that these are solid normal curves in more than two dimensions and their shapes are dependent upon segmental averages of a series of high and low values. Indeed, even in moisture situations where a particular species appears to reach its optimum, it may be absent from particular stands, be a dominant in its particular layer in others, or be weakly represented, depending upon the combination of environmental factors. Its

absence in stands apparently suited to its existence may be partially accounted for on the basis of historical effects, fortuitousness of establishment, the strong influence of intraspecific or interspecific competition, or again our misconceptions of the resultant of many important environmental factors.

In graphing these species relationships only a few were chosen from those available. These have been so selected to provide an indication of the type of species reaction which exists in relation to the moisture gradient. Limited space prevents a more extensive graphic presentation than would be desirable. As may be confirmed by referring to Table 2, which presents the quantitative averages in relation to the moisture gradient, many other species could have replaced those presented in the graphs, to illustrate the same type of relationships. Even those species for which only sparse data are available, show the normal distribution or some slight aberration of it, as the most frequent type of relationship. For the graphs, it should be mentioned that no smoothing procedures were performed. The very close similarities to regular normal curves are the product of a simple average of values for all stands in each moisture segment.

In Fig. 2 the average importance values for *Picea glauca* and *Abies balsamea* are presented with those of three other significant tree species, in relation to the moisture gradient. Both species attain a high level of importance and at the same time illustrate a broad range of tolerance to all moisture conditions of the gradient. Even though their ranges overlap along the entire series, each possesses a clearly differentiated tendency to attain optimum importance at only one end of the gradient; *Picea glauca* on the drier sites, *Abies balsamea* in the wetter situations.

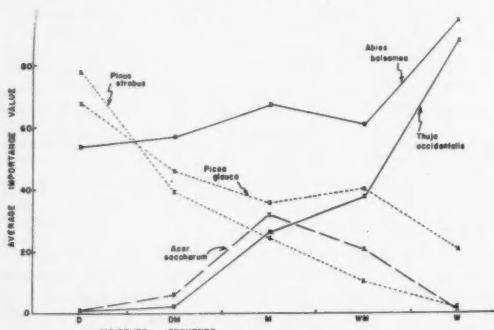


FIG. 2. Curves representing the distributions of importance values, averaged for moisture segments of the moisture gradient, for 5 of the leading dominants.

Neither species tends to attain its peak of importance in the mesic portion of the gradient. *Thuja occidentalis*, like *Abies balsamea*, tends to attain maximum importance at the wet end, but it is much more restricted at the dry end. The curve for *Pinus strobus* is similarly related to that of *Picea glauca*. Notice that this species has no peak in mesic situations as

would be expected of a climax member. The importance average for *Pinus strobus* in the mesic segment is largely derived from values for large scattered specimens in predominantly hardwood stands. *Acer saccharum*, unlike any of the other 4 species, reaches optimum development on mesic sites although it is distributed over an extensive range of the moisture series.

Various other tree species did not attain the level of importance of the 5 species referred to above, but were nevertheless important in community structure. Their relationships are presented in Fig. 3 with the curve for *Acer saccharum*. The broad range of tolerance illustrated by *Betula papyrifera* and *Acer rubrum*, is in marked contrast to the narrower amplitudes of *Pinus resinosa*, *Acer saccharum*, *Tsuga canadensis* and *Betula lutea*, although these species are by no means sharply restricted. The tendency for each species to reach its highest level of importance in a particular moisture segment is readily apparent, but at the same time this occurs independently of the various levels of importance attained by any single species, or the overlapping and intergrading amplitudes of tolerance.

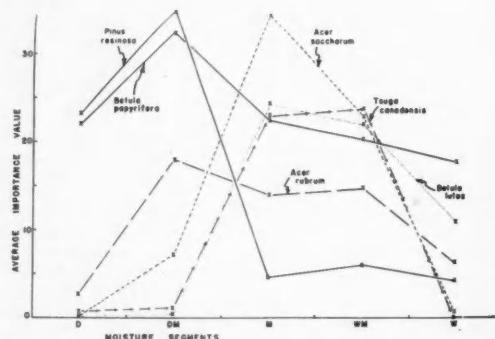


FIG. 3. The distributions of importance values, averaged for moisture segments of the moisture gradient for tree species of significant occurrence.

The relationships of lesser tree components are graphed in Fig. 4. The same types of trends exhibited by the more significant tree species, apply equally well to these, namely, the ability to indicate preference for particular moisture situations and to display maximum development in these situations. The ranges of *Ostrya virginiana*, *Tilia americana*, *Fagus grandifolia*, *Quercus rubra* and *Pyrus americana* tend to be somewhat more restricted than those of most of the important species.

The fact that certain groups of tree species tend to develop optimally in the same moisture segments is worthy of note. *Picea glauca* and *Pinus strobus* attain importance in dry conditions, *Pinus resinosa*, *Betula papyrifera*, *Acer rubrum*, *Populus grandidentata* and *Quercus rubra* in dry-mesic conditions, *Acer saccharum*, *Betula lutea*, *Tilia americana* and *Fagus grandifolia* in mesic conditions and *Tsuga canadensis* and *Populus balsamifera* in wet-mesic

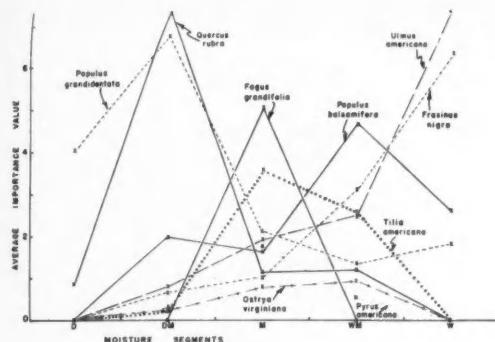


FIG. 4. Importance curves for minor tree species on the moisture gradient.

situations. In a similar manner *Abies balsamea*, *Thuja occidentalis*, *Ulmus americana* and *Fraxinus nigra* attain their significant importance in wet situations. In considering these relationships it should be remembered that most of these same species do mingle with each other along all portions of the moisture gradient, albeit in different proportions in different situations. In short, the over-all continuity of the vegetational complex is as markedly evident as the arbitrary vegetational segments under different moisture influences. If the tolerance curves for all tree species could be incorporated into a single graph in the absence of complexity, it would be clearly evident that all curves would intergrade and each, or a portion of each, would tend to attain an optimum in a particular segment of the moisture gradient. The relation of any single species would apparently be independent of the relations of others.

Populus tremuloides, *Betula papyrifera*, *Populus grandidentata* and perhaps *Populus balsamifera* are usually considered as pioneer species due to their rapid invasion and successful establishment following fires and large scale disturbances. The importance values for these species (Table 2) show that the two latter species occur at approximately the same level of importance throughout the gradient and were never important dominants over extensive areas. The reverse is true for *Betula papyrifera* and *Populus tremuloides*. The former dominated 4 stands and the latter 5, but these species occur in pure stands or in mixture over thousands of acres of forested land in the Lakes region. Along the moisture gradient both *Populus tremuloides* and *Betula papyrifera* attain high levels of importance in any moisture segment, indicating their capabilities of invading even mesic areas which have suffered disturbance and where available light energy is plentiful. Although both species are extremely intolerant and lack the ability to persist when invaded by other species, they may occupy openings in almost any type of stand. Apart from the level of importance attained, all of these species tend to prefer a particular moisture segment, but *Betula papyrifera* and *Populus tremuloides* have

the ability to invade and occupy disturbed sites, regardless of moisture conditions.

The relationships of *Picea mariana* and *Pinus banksiana* to the moisture gradient are presented in Fig. 5. The bowl-shaped distributions which result from the averaging of importance values in sequential segments are in contrast to the normal distributions postulated for the ecological tolerances of plants to environment. That both species apparently tend to reach optima in both the dry and wet portions of the gradient would seem to indicate a conflict of ecological preferences.

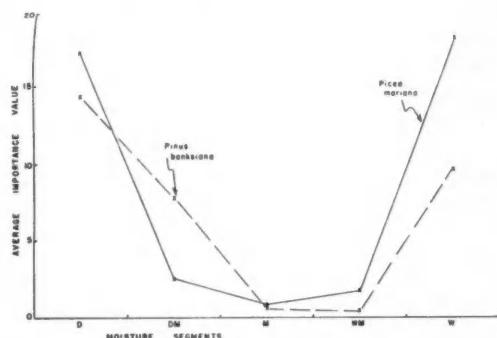


FIG. 5. Importance values for *Pinus banksiana* and *Picea mariana*, averaged for each segment of the moisture gradient. The bowl-shaped amplitudes of tolerance, with both species apparently attaining optima in both dry and wet conditions would seem to indicate conflicting ecological preferences.

No particular attention was paid to the stage in successional development of any stand when selected for survey in the field. When the main criteria for stand selection were decided upon, due consideration was given only to selecting as wide a variety of forest composition as exists in the area of study. Although there has apparently been little if any agreement among the ecologists who have studied isolated local areas of vegetation in the Great Lakes region, as to the paths of successional development and the ultimate climax or terminal stages, it is a certainty that the 110 forest stands studied at random must represent a major portion of the successional gamut. However, the ecological characteristics and successional tolerances of many of the tree species involved have been considered and the moisture gradient does provide a satisfactory basis for a discussion of these relationships within the framework of community structure. With this purpose in mind the quantitative relationships of saplings to trees of the canopy have been compiled and are presented in Table 4. Average relative density of saplings is compared to average relative density of trees for the same species, for the various moisture segments for 6 of the more important species.

These data illustrate effectively that tree reproduction is distributed on the gradient in patterns similar to those of the mature trees. Thus, where

TABLE 4. Comparison of tree reproduction (saplings) and mature trees in 103 Upland Stands—Great Lakes Region.

Species		AVERAGE DENSITY PERCENT				
		D	DM	M	WM	W
<i>Picea glauca</i>	Trees	21.7	15.0	10.2	12.0	5.3
	Saplings	12.7	7.0	7.0	5.8	1.6
<i>Abies balsamea</i>	Trees	22.6	21.1	26.4	23.4	37.5
	Saplings	46.6	35.6	38.9	31.0	35.8
<i>Acer saccharum</i>	Trees	0.1	1.5	11.2	7.7	0.1
	Saplings	0.1	5.4	19.4	11.4	0.4
<i>Populus tremuloides</i>	Trees	5.1	15.4	5.7	9.7	5.2
	Saplings	3.6	9.4	1.5	3.3	1.3
<i>Betula papyrifera</i>	Trees	6.2	9.7	6.5	5.6	4.8
	Saplings	3.4	8.3	3.1	5.0	3.3
<i>Pinus strobus</i>	Trees	22.8	11.9	7.1	2.3	0.3
	Saplings	6.6	3.4	1.1	0.5	0.2

moisture conditions appear suitable for trees of a species, they are similarly suited to the saplings. Certain other tendencies have been somewhat obscured in the process of averaging but nevertheless appear quite clearly. For *Pinus strobus*, *Betula papyrifera*, *Populus tremuloides* and *Picea glauca*, sapling values invariably fall well below the level of the mature trees. This is especially true for *Pinus strobus* on the dry sites where relative density of reproduction is approximately 25% of the relative density for trees. All these species will ultimately play less important roles in the canopies of the stands represented, provided no serious disturbances reverse successional developments now in progress. The reverse situation appears to hold for *Acer saccharum* and *Abies balsamea* which will play more important roles. The data for *Abies balsamea* are less reliable in this respect than that for *Acer saccharum*. In dense canopy stands, many of the *Abies balsamea* saplings of the samples were in an unhealthy and suppressed condition due to continued and severe shading, but were still living. Often in thickets of saplings in such situations, several individuals nearest to the point in each quadrant had succumbed and it was difficult to select living specimens. In contrast saplings of *Acer saccharum*, even though they may have been heavily suppressed, seldom appeared unhealthy and dead specimens were not common.

In those stands composed predominantly of hardwood species, saplings of all conifers, except *Abies balsamea* as described, were conspicuous by their absence. When present, the conifer saplings often occurred in somewhat open and disturbed situations. While it is often unwise to place complete reliance on quantitative data of tree reproduction, it is true that for most of the areas visited, the data show trends toward increasing quantities of hardwood species and decreasing amounts of conifers, in the absence of frequent or widespread disturbance.

Many difficulties were met with in attempting to portray graphically the reactions of herbaceous and shrub species to the moisture gradient. These species are of course much more numerous than the trees and

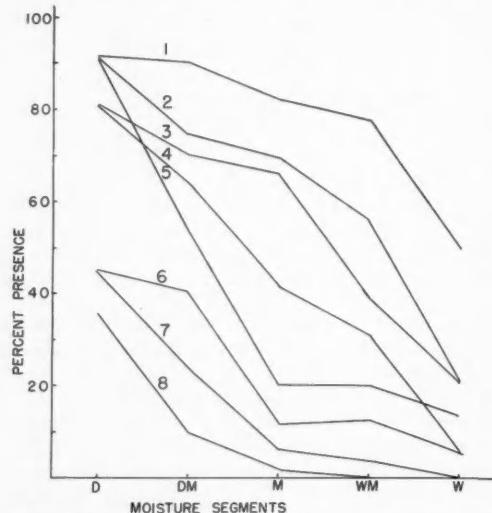


FIG. 6. Distribution of presence values, averaged for the 5 segments of the moisture gradient, for species tending to attain optimum development in dry moisture conditions. 1. *Corylus cornuta*, 2. *Amelanchier* sp., 3. *Lycopodium obscurum*, 4. *Apocynum androsaemifolium*, 5. *Pinus resinosa*, 6. *Chimaphila umbellata*, 7. *Antennaria* spp., 8. *Comptonia peregrina*.

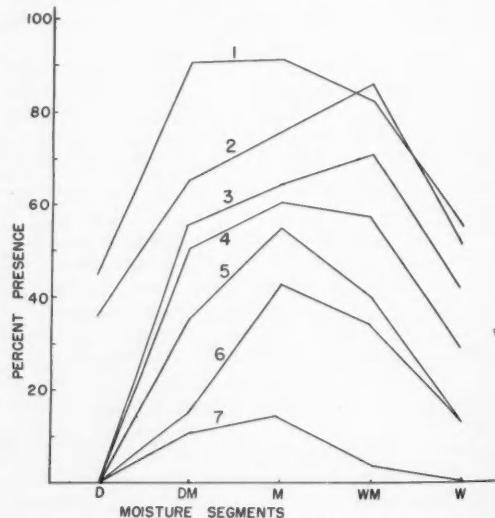


FIG. 7. Distribution of average presence values for understory species tending to reach optimum importance in mesic moisture conditions. 1. *Streptopus roseus*, 2. *Viola incognita*, 3. *Athyrium felix-femina*, 4. *Brachelytrum erectum*, 5. *Osmorrhiza claytoni*, 6. *Rubus parviflorus*, 7. *Mertensia paniculata*.

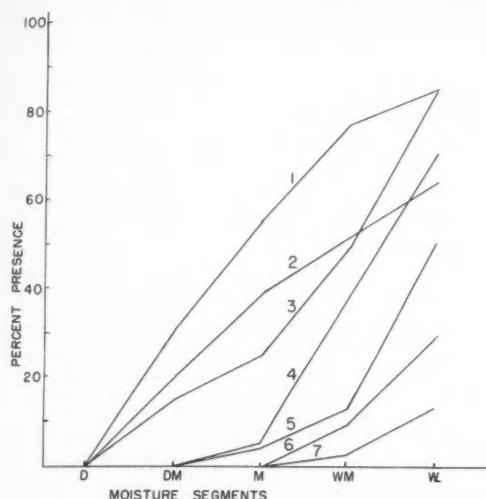


FIG. 8. Presence values for understory species, averaged for segments of the moisture gradient and attaining optimum importance in wet moisture conditions. 1. *Mitella nuda*, 2. *Circaeal alpina*, 3. *Alnus rugosa*, 4. *Viola pallens*, 5. *Lycopus uniflorus*, 6. *Habenaria hyperborea*, 7. *Cicuta maculata*.

a variety of relationships is available. While only the relationships of a selected group of species are graphed, Table 3 clearly indicates the numbers of species which are available to support the type relationships presented in Figs 6 to 8. Explanations of these graphs are not required since they are quite simple and self-evident.

In Fig. 6 the relationships of a group of species, based on percent presence values for each moisture segment are presented. Note the same general trends in that all attain optimum development or "peaks" in the dry segment, and at the same time much reduced influence in the wet segments of the gradient. A similar graphic presentation is provided for groups of species attaining their highest level of importance in mesic (Fig. 7) and wet segments (Fig. 8). Table 3 indicates that many similar graphs for many species, based on averages obtained for frequency or presence values along the gradient, could have been prepared to show a tendency toward optimum development in any one of the 5 moisture classes.

The few typical graphs presented are sufficient to illustrate that any particular species finds conditions most suitable for development within a specific range of moisture conditions, and this tendency is apparently independent of the distributions of other participants in the community complex. Some species are more restricted by moisture conditions than others as is reflected in a narrower amplitude of the normal curve. If the many species curves available were to be incorporated in a single composite graph, it would show groups with similar tolerance patterns but each would differ from every other in the shape of its

tolerance curve and no two groups of exactly similar behavior would be present.

Of those species which peak at extreme ends of the moisture gradient, many are represented by partial tolerance curves and pass off the gradient. Many appear to attain optimum development in either the dry or wet segments, but others apparently peak in situations of moisture outside the limits represented in the gradient. Such is actually the explanation for partial responses. If data for stands dominated by *Pinus banksiana*, which often occur on severely drained sands and gravels in open dry situations where *Picea glauca* and perhaps *Abies balsamea* would seldom be found, were included in an additional "very dry" segment, curves for many of these species on the dry end would probably continue to rise to an optimum in the adjacent drier segment. If stands in swamp situations characterized by the accumulation of atmospheric moisture, were included in an additional "very wet" category adjacent to the wet segment, the species previously described would be similarly continuous and grade into these very wet situations. The apparent absence of *Picea glauca* from these two extreme situations, at least in stands of at least 10 A in size, precluded the inclusion of such data in this study. What is then apparent, is that only a portion of an even more extensive continuous vegetation complex is being dealt with, and such examples indicate these inseparable relationships.

A group of species which are often considered to be of greater importance in the deciduous forest communities in more southern areas were seldom encountered in boreal conifer-hardwood stands in the Lakes region. The percent presence values for 40 such species in the moisture segments are presented in Table 5. That these species barely penetrate this more northern community is evidenced by their low percent presence values. In general they possess a very limited range of tolerance on the gradient, being often confined to a single or adjacent moisture segments. All species are not confined to any group of segments but show a continuous gradation from dry to wet situations with considerable overlap throughout. These relationships would be expected of species on the edge of their geographical and ecological ranges. They do indicate the continuous relation which exists between these adjacent regional vegetation types.

Not all herbaceous and shrub species are distributed along the gradient in a manner represented by a simple normal distribution. A large number of species portray relationships similar to those shown for *Pinus banksiana* and *Picea mariana*. Their bowl-shaped distributions, indicating a preference for both the dry and wet situations, are presented in Fig. 9. *Epigaea repens*, *Larix laricina*, *Gaultheria hispida*, *Salix* sp., and *Vaccinium angustifolia*, show relationships quite similar to those graphed. The fact that these species are thought to possess high acidity requirements should be mentioned.

Another extensive group of species is represented by decidedly bimodal curves. The relationships which

TABLE 5. Percent presence values for species which attain greater importance in more southern vegetation types. That these species barely penetrate the spruce-fir-mixed hardwoods community complex is evidenced by the low values, confined to only limited segments of the moisture gradient.

	D	DM	M	WM	W
<i>Panax quinquefolius</i>	1	—	—	—	—
<i>Juniperus communis</i>	9	—	—	—	—
<i>Trillium erectum</i>	9	—	—	—	—
<i>Hamamelis virginiana</i>	9	10	—	—	—
<i>Pedicularis canadensis</i>	9	5	2	—	—
<i>Corylus americana</i>	9	5	—	4	—
<i>Quercus alba</i>	9	5	—	9	—
<i>Parthenocissus quinquefolia</i>	—	10	2	—	—
<i>Sanguinaria canadensis</i>	—	10	2	—	—
<i>Smilax tamnoides</i>	—	10	2	—	—
<i>Ulmus rubra</i>	—	5	5	—	—
<i>Anemone virginiana</i>	—	5	5	—	—
<i>Quercus macrocarpa</i>	—	10	5	4	—
<i>Carpinus caroliniana</i>	—	5	2	9	—
<i>Caulophyllum thalictroides</i>	—	5	10	9	—
<i>Hepatica acutiloba</i>	10	—	4	—	—
<i>Carya cordiformis</i>	5	—	4	—	—
<i>Gaultheria lanceolatum</i>	5	—	4	—	—
<i>Acer negundo</i>	—	—	7	—	—
<i>Claytonia caroliniana</i>	—	—	5	—	—
<i>Cryptotaenia canadensis</i>	—	—	2	—	—
<i>Dicentra cucullaria</i>	—	—	2	—	—
<i>Erythronium americanum</i>	—	—	2	—	—
<i>Gaylussacia baccata</i>	—	—	2	—	—
<i>Isopyrum biternum</i>	—	—	2	—	—
<i>Orchis spectabilis</i>	—	—	2	—	—
<i>Rhus typhina</i>	—	—	2	—	—
<i>Allium tricoccum</i>	—	—	2	4	—
<i>Medeola virginiana</i>	—	—	7	4	—
<i>Panax trifolius</i>	—	—	7	9	—
<i>Geranium maculatum</i>	—	—	5	9	—
<i>Adiantum pedatum</i>	—	—	2	13	—
<i>Desmodium glutinosum</i>	—	—	—	9	—
<i>Hystrix pumila</i>	—	—	—	9	—
<i>Podophyllum peltatum</i>	—	—	—	4	—
<i>Anemonella thalictroides</i>	—	—	—	4	—
<i>Heuchera richardsonii</i>	—	—	—	4	—
<i>Hydrophyllum virginianum</i>	—	—	—	4	—
<i>Laportea canadensis</i>	—	—	10	4	7
<i>Dentaria diphylla</i>	—	—	—	—	7

these curves indicate are not particularly clear. A great many of these species decrease in importance in the mesic segment in which a large percentage of the stands are dominated by hardwood species. These herbs and shrubs apparently cannot successfully withstand the conditions existing in such situations, but whether it is a matter of a more basic soil reaction, the effects of litter type, the manner of leaf fall, or some other factor, is not clearly evident. The graphs for representative species of this type are provided in Fig. 10.

One group of species attained a high level of importance throughout the entire range of moisture conditions and the curves indicating their relationships to the gradient are accordingly not characterized by any marked optimum values. The graphs for 9 species of this type are shown in Fig. 11. *Maianthemum canadense* is a representative of the group. It was present in every one of the 110 stands and occurred with an average frequency of 66% in the

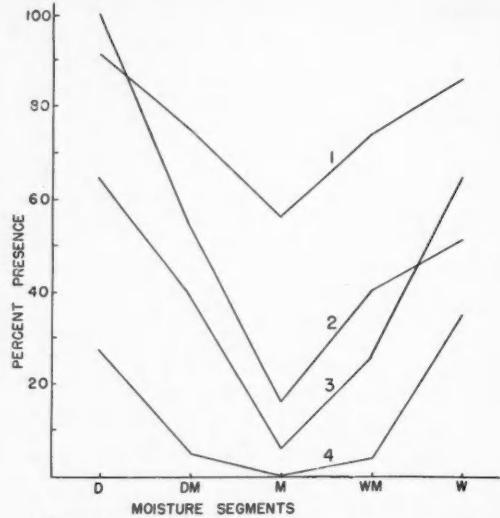


FIG. 9. Species indicating apparent preference for conditions at opposite ends of the moisture gradient, as illustrated by bowl-shaped distributions. Distributions based on averages of presence values for each moisture segment. 1. *Linnæa borealis*, 2. *Vaccinium myrtilloides*, 3. *Pinus mariana*, 4. *Ledum groenlandicum*.

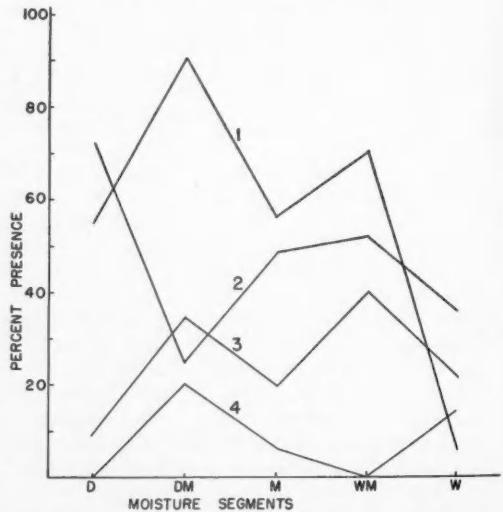


FIG. 10. Understory species displaying bimodal distributions along the moisture gradient. Based on presence data. 1. *Oryzopsis asperifolia*, 2. *Lycopodium annotinum*, 3. *Thalictrum dioicum*, 4. *Lysimachia ciliata*.

dry segment and decreased gradually to a value of 44% at the wet end. The majority of these species are represented by flat or straight line presence curves and their frequency curves often indicate no marked deviation from the trends illustrated by the presence curve. In most instances it appears that they would find optima and subsequently decline in importance

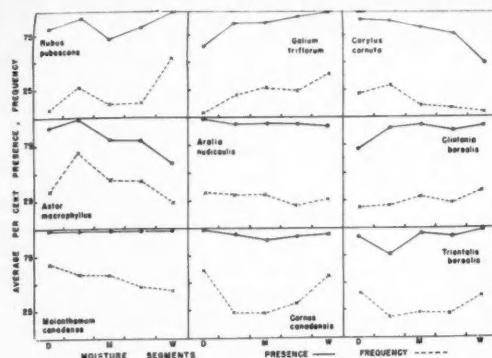


FIG. 11. Species attaining a high level of importance in the community. Curves are based on both presence and frequency data as averaged for segments along the moisture gradient. Note the similarity between the frequency and presence curves in each instance. Their curves indicate the unsuitability of these species to differentiate moisture conditions within the environmental limits of this study.

in situations of site moisture not represented in the present gradient. The very high levels of importance attained and the lack of significant trends sharply reveal their inconsequential value as indicators of moisture condition or particular combinations of tree species. These species have been often employed for such purposes in forest classification systems however (Heimbigner 1934, 1941; Westveld 1930, 1953; Ku-jala 1945; Cajander 1926; Linteau 1955).

The relationship of presence to frequency for a number of species adapted to various moisture segments is provided in Fig. 12. Frequency curves have also been included in Fig. 11 for those species with high importance throughout the moisture gradient.

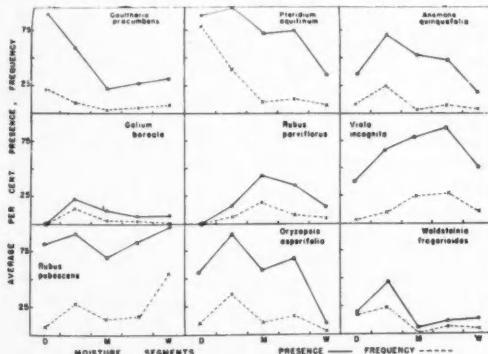


FIG. 12. Curves for species, based on averages of both presence and frequency values in each of the segments of the moisture gradient. The curves for these plants have been selected to indicate the remarkable similarities which consistently occur between these measurements for species within the community.

The relation existing between these two quantitative characteristics is of value from the standpoint of

the effectiveness of each in describing vegetation and to decide whether they augment each other with respect to purpose. Although the species in Fig. 12 were selected for this purpose at random from Table 3, it is apparent from the table, that these same close relationships generally exist for almost all species. In a few instances there were discrepancies, but the overall picture was seldom distorted. Often, frequency values for the rarer species were of little use to indicate species moisture preferences but frequency often furnished a more exact picture for those species with moderately high presence values. Knowledge of presence-frequency relationships can be a valuable aid to phytosociological sampling techniques since, if one corroborates the other, recording of presence alone might be justified.

In Fig. 13 the presence curves for 3 species of the genus *Goodyera* are provided. Notice that the ranges of tolerance of these closely related species differ markedly with respect to moisture preferences.

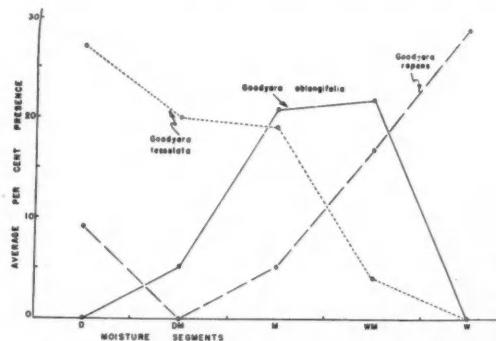


FIG. 13. Tolerance curves for species of the genus *Goodyera*, based on presence values averaged for segments along the moisture gradient. Note that each peak in different sections of the gradient and yet there is a continuous overlapping of curves to indicate that no species is entirely distinct with respect to its relationship to various moisture phases of the community.

G. tesselata tended to attain optimum development in the dry segment, *G. repens* in wet situations, while *G. oblongifolia* predominated on mesic sites, yet there are intergradations at most points along the gradient. This situation exists for many member species of the same genus, especially in those genera represented by a number of species, as for example *Aster*, *Cornus*, *Solidago*, *Viburnum*, *Viola*, *Lycopodium*, *Rubus*, *Carex*, *Smilacina*, and others. That such knowledge is of unquestionable worth to present day taxonomic treatments of genera is evident. The inclusion of quantitative data indicating the ecological tolerances of species, would greatly improve the monographic treatment of genera.

ENVIRONMENTAL CORRELATIONS

The correlation of environmental factor measurements with plant distribution and growth presents a complex problem as all experienced field ecologists

will realize. The plant physiologist often experiences difficulty in interpreting the results of carefully organized experiments dealing with mineral deficiencies, conducted in the greenhouse under closely controlled conditions of light, moisture and nutrients, and employing plants, for which an extensive amount of life history data have accumulated. The difficulties of the ecologist in the natural environment, complicated by a multitude of factors can thus be well understood. The data for environmental measurements were averaged (Table 6) for the various moisture segments in an attempt to determine whether these characteristics presented continuous patterns to the gradient as did plant species and as a step toward correlating plant distribution with environmental characteristics.

TABLE 6. Summary of environmental characteristics averaged for moisture segments along the moisture gradient. Based on 100 Stands.

Factor	Dry	Dry-Mesic	Mesic	Wet-Mesic	Wet
Moisture Retaining Capacity (% dry wt.)	161.3	198.6	223.0	247.3	365.0
pH.....	4.5	4.8	4.6	4.9	4.5
Ca lbs/acre.....	917.5	3943.9	3520.0	6837.5	7592.3
Mg lbs/acre.....	150.0	463.6	409.6	543.8	588.5
K lbs/acre.....	178.5	204.6	206.1	246.3	340.4
NO ₃ lbs/acre.....	1.0	2.5	8.3	7.6	1.0
NH ₃ lbs/acre.....	28.0	37.7	42.8	36.6	37.7
P lbs/acre.....	50.0	62.7	52.6	50.6	45.4
Depth A ₃ (inches)					
Average-3 stations.....	2.4	1.6	2.0	2.1	3.3
Depth A ₁ (inches).....	0.5	1.5	1.6	3.5	5.6
Depth A ₂ (inches).....	2.2	2.3	2.3	1.4	0.9

Since considerable reliance was placed in site moisture as a determiner of community patterns, a correlation of moisture retaining capacity of the soil with the moisture gradient was naturally expected. A high degree of correlation was not necessarily essential however, because moisture retaining capacity is indicative only of the retentive properties of soil and not necessarily the moisture conditions of the site at any one period. The values for moisture retaining capacity along the gradient (Table 6) indicate the high correlation obtained, with a gradual increase from 161 in the dry segment through 223 in the mesic to 365 in the wet segment. The smooth curve represented by these gradually increasing values is adequate to support the ordering of stands in broad moisture classes on the basis of a knowledge of the moisture conditions of site, as gained from field experience. Such information could be profitably used to produce a purely objective ordination of stands except for a few special cases where personal judgment would have to be exercised. It should be emphasized that the data for moisture retaining capacities were not available until the grouping of stands had been completed. The value of the ordination at that time had to be decided solely on the basis of floristic relationships. Thus moisture retaining capacity data were not at hand to prejudice this phase of the ordination but its subsequent value as a

test of the suitability of the ordering of stands is certainly apparent.

The relation of soil pH to the gradient is complex, with the occurrence of a decrease in the mesic sections. pH values were converted to arithmetically equivalent values, then averaged for various moisture segments and then the average reconverted to a pH value. These final pH values were comparatively high in both the wet and dry segments and lower in the dry-mesic and wet-mesic segments. It should be noticed that there is only a slight overall difference between the highest and lowest of these pH values (4.5-4.9) and this range, if it does have significance is therefore not great. Larger differences did occur between individual stands, with pH values ranging from 4.0 to 7.0.

The question of whether these environmental factors are a direct cause or a result of the type of vegetation supported, or whether they are a combination of both, may be posed in the case of most factors presented, but particularly so in a consideration of soil pH.

Chemical analyses of the humus and A₁ layers for 10 stands chosen at random indicated that both layers are similar in respect to most nutrients tested for, but the humus layer is apparently frequently richer in calcium, phosphorus and potassium and perhaps contains smaller quantities of magnesium. The two layers are separated only with difficulty since the A₁ layer is almost always poorly represented. The humus layer in these stands is the site of considerable plant activity and this tendency is supported by the high representation of hemicyclopediae in the life-form spectrum.

The series of values for other environmental characteristics, especially those for the soil nutrients, magnesium, ammonium, calcium, phosphorus, potassium and nitrogen (nitrate), show trends in relation to the moisture ordination and reach high levels in particular segments in a somewhat similar fashion to the plant species. Each characteristic has its own pattern and undoubtedly correlations exist in relation to the overall environmental complex and the vegetational components of particular segments of the gradient, but an interpretation must be postponed until more thorough methods of sampling and treatment of data are utilized.

In the study of vegetation the primary considerations are: an inventory of the plants which occur together to give some semblance of a community; the quantitative occurrences of individual species; their relations to each other; and relationship to the environment. Thus the analysis or treatment decided upon should shed light upon these aspects of the community and then provide a sound basis for further autecological studies. The test of the analysis of course lies solely in the soundness of the results.

The tables of data and the curves of individual species in relation to the moisture gradient demonstrate that reasonable patterns were obtained. The majority of these curves are of the smooth normal type expected and accepted in biology as indicating

the relations of organisms to the natural environment. This in itself is sufficient to support the arrangement of stands decided upon, but additional proof is furnished by the results of an analysis of moisture retaining capacities. The smooth curves for other environmental factors and mineral nutrients must also be weighed in any appraisal of the ordination.

Certain difficulties were encountered during the moisture gradient analysis however. In a few instances it was difficult to decide upon the moisture characteristics of individual stands. Important determining factors other than moisture were indicated by the peculiar bowl-shaped and bimodal curves obtained for many species. Explanations could often be provided to explain these peculiarities, but frequently conflicting interpretations arose in the same situation. It was realized that many of these peculiar situations were simply the outcome of viewing a multi-dimensional phenomenon in only two dimensions. The method itself was partially subjective, and necessarily so, since the moisture gradient could not have been reasonably established without considerable field experience, although an ordination based on moisture retaining capacities would no doubt have provided similar results.

An important source of difficulty was recognized in the field and during the analysis, and is due primarily to the inherent characteristics of the vegetation. It was early recognized that the trees apparently do not influence ground cover in mixed boreal conifer-hardwood vegetation in this region to the extent they might in vegetation farther south. Often the same type and composition of tree cover is accompanied by markedly different combinations of herbs and shrubs in the undergrowth. This situation might perhaps indicate that the community is primarily composed of the herb, shrub, moss and lichen layers, and that the trees, apart from their effect on overall environment, are incidental members. This interpretation is partly supported by a consideration of succession in this region. If an area is disturbed, the initial tree layer will be predominantly influenced by the degree of disturbance rather than the moisture conditions of site. At the same time, if the disturbance has not been of a magnitude sufficient to effect a marked change in the moisture conditions of the site, the initial herb and shrub layer of the post-disturbance period will probably be similar to that existing before the disturbance. Such considerations are of great importance in an area where there can be every degree of disturbance from a fire which reduces the substrate for forest growth from a deep humus to bare rock, to one in which only a few scattered canopy members are destroyed by wind or a light infestation of spruce-budworm.

With these conflicts in mind, the question arose as to whether stands could not be ordinated on a purely objective basis, utilizing phytosociological characteristics, that is the quantitative aspects of species themselves, and whether such arrangements might not better explain certain difficulties and reveal other dimensional patterns if such existed. The quantita-

tive data for herbs and shrubs seemed more valuable in this respect than that for the trees, since many seemed more restricted by moisture and for the reasons cited above. The recent work of Bray (1956) and Bray & Curtis (1957), in a somewhat modified form, seemed suitable for this situation and a three-dimensional phytosociological treatment was attempted.

THREE-DIMENSIONAL ORDINATION

The general procedure in such ordinations is to decide upon some index for assessing stand similarity and then on the basis of index values derived from stand comparisons, position stands in quantitative spatial relation to each other. If the index utilized is to be phytosociologic it must be based on the quantitative relationships of groups of species which are peculiar to the community studied. Thus a group of species is selected and the values for each stand are converted to relative values based on occurrences in all stands. Then score values are derived by converting these relative values to values relative to the complement of species in each stand. Stands are then compared to each and every other stand, recording the lower of the two score values for all species in common to both stands, and such values are finally summed as an index of similarity. High totals so obtained indicate close similarity and zero values result when two stands have no species in common. All stands are compared in this way with all other stands and the resulting table of all comparison values forms a complete matrix. This complete matrix is then employed to determine the opposite ends of the primary ordination axis. The calculation of a complete matrix presents no difficulty provided a great number of stands are not involved since the number of comparisons required increases in geometric proportion to the increase in stands.

An alternate and simplified procedure involves the calculation of a partial matrix. All values of the complete matrix are calculated only in attempts to determine the two most unlike stands, which become the opposite ends of the primary axis. If one is sufficiently acquainted with the data to permit the recognition of these stands, or groups of stands containing them, then only a partial or incomplete matrix need be calculated.

In this instance the most floristically dissimilar stands were known to be situated in the wet and dry segments at opposite ends of the moisture gradient and this knowledge permitted the calculation of a partial matrix.

The first step in constructing the partial matrix was to determine the groups of stands among those of the dry and wet segments which floristically represented these moisture extremes. An herbaceous indicator index (Curtis 1955), was calculated for all stands of the dry and wet segments to arrange them in order of decreasing dryness and wetness. Fifty species of herbs and shrubs were selected for this purpose, 10 from each of the 5 moisture segments. Only those species represented by binomial amplitudes of tolerance, with neither very high nor de-

ecidedly low values along the gradient, and which attained optimum development in the segment concerned, were chosen. These 5 groups were weighted by assigning a value of 1 to the dry species, 2 to the dry-mesics, 3 to the mesics, 4 to the wet-mesics and 5 to the wet species. In each of the stands of the dry and wet segments, any of the 50 species when present, was assigned the weighted value. These weighted values were summed and divided by the number of such species present, in each stand, to yield the index. The driest stand was represented by the lowest and the wettest stand by the highest index. The 5 stands with the lowest indices and the 5 with the highest indices were employed in constructing the partial matrix.

Before the matrix could be calculated it was necessary to select a group of species to be used in calculating individual stand scores and to serve as a sample to compare the similarity between individual stands. Those 50 species used in the herbaceous indicator technique, plus 10 strongly bimodal species and the 12 most important tree species, 72 in all, were used in this regard. Both actual density and actual dominance were listed for tree species to weight the scores in favor of the community dominants. Special forms were prepared for the calculation of scores and to aid in the rapid comparison of stands.

The procedure followed in calculating score values was as follows. Absolute density and dominance per acre for each of the 12 tree species in each stand were recorded. Frequency values for herbs and shrubs were also listed as they occurred in the stand data. Then each of these values separately was calculated as a percent of the maximum value for each species in all 102 stands used, to produce an actual score. For example *Abies balsamea* attained the highest density value, 581 trees per acre in stand number 90. This value was considered as 100% and all of the 101 other density values for this species were transformed to a percentage of this value. This procedure was necessary because the individual values for all species were in different units, since the measurements were made using different methods. This difference was rectified by expressing each value as a percentage of the maximum value attained for the species in any of the stands. However, these actual scores could not be directly used in stand comparisons since the number of scores and the sum of these scores varied from stand to stand. These actual scores were accordingly summed for each stand individually and each value was calculated as relative to this sum of actual scores. These final scores were then transferred to special comparison forms.

The 10 stands previously selected using the herbaceous indicator technique (the 5 driest and 5 wettest stands) were then compared individually with every other stand, and the lower scores for species in common (or the same score for common species with identical values) were totalled in each comparison. The result was a sum of a series of numbers representing the lower of the values for all species com-

mon to the two stands of a comparison, on the form. This value ranged from 0 to 100 depending on how similar the two stands were. All of these values were entered in the partial matrix.

To determine the position of stands along the primary axis, the 10 rows of partial matrix were totalled and the stand represented by the lowest of these totals was the stand most unlike all others. It became one end of the axis. The matrix values for this stand were then examined and the stand having the lowest comparison value in relation to it became the opposite end of the axis.

The next step was to ordinate each of the other 100 stands, on the basis of their similarities and differences to these 2 stands, in such a way that the most similar stands were closest to each other and the most dissimilar most distant. To accomplish this the matrix values for the end stands were examined and the highest value in either was selected. All of the matrix values for the stand chosen as the second end of the axis were subtracted from the highest value. The values so obtained were added to the scores for the same stands as obtained in comparison to the stand chosen as the first end of the primary axis, and the sum divided by two. This produced an average value for each stand and stands were subsequently arranged in order of these average values to produce the primary axis. This arithmetic ordering of stands differs from the geometric method of Bray & Curtis (1957).

As so frequently occurs in ordination treatments of this type, the stands designated as the ends of the primary axis were found to be considerably different from all of the other stands. This resulted in an uneven spread of these stands from the other stands in the ordination and made presentation and plotting procedures cumbersome. In an attempt to overcome this difficulty "average" stands were prepared by averaging all final scores for the 5 stands selected from each end of the moisture gradient by the herbaceous indicator technique. The above procedures were then repeated using these "average" stands as the ends of the primary axis. The resulting order of stands did not differ markedly from that obtained by the previous procedure. All stands were in comparatively similar positions in relation to their neighbors and the primary axis produced was more compact.

In a similar manner an ordination along the secondary axis (perpendicular to the first) was accomplished. The midpoint of the primary axis was determined and the 20 stands nearest to it were selected. These stands were then compared with each other resulting in a partial set of matrix values. From this group, the 2 stands which on the basis of these matrix values were most different, were selected as the opposite ends of the secondary axis. These 2 stands were subsequently compared with all stands and the latter were ordered along this axis on the basis of their similarities and dissimilarities to these end stands as indicated by the matrix values and by the method described above for the primary axis. Finally a third dimension was separated by selecting

the 15 stands around the intersection of the midpoints of the primary and secondary axes, calculating their matrix values by comparing each with the others of the group, selecting the two most different stands and then repeating the same ordering procedure employed for the first two axes.

The positions of stands yielded by this three dimensional ordination were then plotted. Since a single page possesses but width and length and lacks the third dimension of height, 3 sheets were necessary in plotting stand positions in all 3 dimensions. The primary and secondary, primary and tertiary, and secondary and tertiary axes were included on single sheets. The actual units separating stand locations are multiples of the values obtained in comparisons and could be reduced proportionately to any scale. The comparable distances separating stands are the important consideration regardless of the units in which they are scaled. Once the stand position was established, this permitted the plotting of actual values for any of the field measurements, importance values, frequency, presence, pounds per acre of calcium, etc., to determine relationships as indicated by the resulting patterns.

Toward this end, 3 sheets with patterns of dots, representing actual stand locations, were prepared. One set was properly labelled with the stand numbers. Additional corresponding sheets could then be placed over these on a tracing table and the data for any species or factor for a particular stand, could be plotted in relation to those for all stands.

This process possessed inherent disadvantages since all stands could not easily be represented in all 3 dimensions contemporaneously. A three dimensional model of the entire complex was then prepared using both sides of a square base, properly sealed, as two dimensions, and wires of proper length to indicate the third dimension. Colored beads of different sizes could be placed on the tops of the wires to represent various quantities and to display patterns if such existed. The three-dimensional design of any species or group of species could be presented effectively by the use of this model.

BEHAVIOR OF PLANT SPECIES

The value of the ordination in assisting to interpret and understand the intricacies of community structure and community interrelationships can of course be assessed only in terms of interpretable species patterns produced on the ordination itself. Thus the plant patterns are the sole indicators of the nature of the community. Many investigators will be in agreement with this statement but will qualify it by emphasizing that an understanding of what a species indicates in terms of environmental requirements must first be acquired by the investigator and this knowledge in turn is prerequisite to interpreting the nature of the community. In the present instance it is believed that the original statement requires no addenda—the qualitative aspects of species when properly related to each other will be sufficient to indicate the nature of the community, and then

permit a detailed investigation of habitat relationships, on an objective basis.

The plotting of quantitative values for particular species in the three-dimensional ordination produces patterns best described as representing spheres or atmospheric distributions. Generally highest values are grouped toward the centers of the spheres and values gradually decrease toward the periphery. This impression is conveyed when the distributions in three dimensions are viewed at one time, as in the model. Values plotted on the sheets usually result in circular patterns with a central core of high values and the lowest values on the circumference. When viewed in only two dimensions low values may be associated with high values at the center but these same stands might well be distantly separated in the other dimension not represented in the particular presentation. It might also be true that stands dominated by a particular species might be adjacent to those containing small representations or where it is completely absent. These circumstances might be explained on the basis of chance factors or might be resolved by a further separation of additional axes.

Since the resulting ordination is based solely upon the quantitative aspects of the group of plants selected, the significance of the separate gradients must be determined on the basis of patterns obtained and a general knowledge of the ecological preferences of species. The patterns resulting from the plotting of certain environmental characteristics are of assistance in this regard.

That the primary axis appears to represent a moisture gradient from dry to wet conditions is not surprising, when it was previously indicated that the most floristically diverse stands were those at opposite ends of the moisture gradient. This knowledge was actually of advantage in delimiting the primary axis but in this connection, only the mathematical values for the 72 plant species determined the final positions of the stands. The moisture classes to which stands were previously assigned in the moisture ordination have been plotted on the primary and secondary axes of the three-dimensional ordination (Fig. 14) in an effort to compare the assigned moisture classes to the relative moisture position as determined by quantitative floristics. It has been possible to place lines to separate groups of stands of the same assigned moisture class, with few if any discrepancies, indicating that groups of stands with similar moisture characteristics lie side by side on the three-dimensional gradient. That these lines are not linear, supports the contention that the axes themselves are not strictly linear. These results would seem to corroborate the separation of stands on the basis of observations of moisture conditions in the field. Actually only a single stand is decidedly misplaced, on the basis of moisture class assigned, the wet one adjacent to the dry segment.

The secondary axis represents a gradational series of stands from those composed almost entirely of coniferous tree species, through those composed of mixtures of conifers and broadleaf species to stands

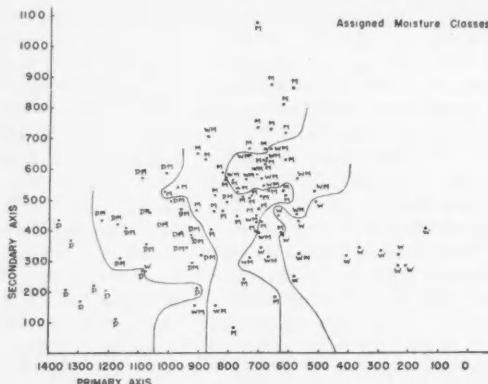


FIG. 14. Distribution of the moisture classes assigned to stands in the moisture gradient analysis, viewed in two dimensions of the three-dimensional gradient. Note that, with few exceptions, the lines separate groups of adjacent stands, each with the same site moisture conditions. This separation along the primary axis of the moisture gradient treatment and indicates that the primary axis is essentially one of moisture extremes.

predominantly deciduous in character. Just what this series represents in terms of controlling environmental influences cannot now be stated. It may be indicative of a temperature gradient or a successional series. A group of stands representing young successional stages and dominated by *Populus tremuloides*, *Betula papyrifera*, *Pinus strobus*, and *P. resinosa*, pure or in mixtures, are closely associated in a relatively small portion of this gradient.

A series of environmental characteristics, requiring separate consideration, indicated trends along the tertiary axis. Soil pH increased in one direction and total calcium (lbs per acre) also increased in the same manner. Other nutrients displayed increasing or decreasing trends along this axis but it is impossible to state exactly what comprises the most influential factor and indeed it is undoubtedly a multiple factor situation.

In any efforts to resolve more completely the various factors represented in these three or any of the additional multi-dimensional axes, and to obtain a more complete understanding of their nature, more exacting environmental measurements would be required and the actions of many more species on the gradient would need to be plotted, than can presently be included. The results at hand however, are sufficient to indicate the fruitful nature of this type of investigation. That the many species available can be shown to be interrelated in multidimensional patterns, approaching somewhat the situation considered to exist in nature, is certainly a promising phytosociological trend.

An additional statement should be made concerning the relative positions of the axes. There appears to be a deviation from a situation in which all derived axes are perpendicular to each other. This deviation appears to increase for each successive axis.

The causes responsible for this state of affairs are not presently recognized or understood and their solution will have to await further investigation. The interrelations of controlling environmental factors and the improbability of independent action on the part of any single factor may partially account for this deviation.

Patterns representing the action of many of the important tree species are provided in Figs. 15 through 22. The importance values for *Abies balsamea*, one of the major tree species, and one used in the ordination itself, and for *Pyrus americana*, a very minor canopy component which had no part in the ordering of stands, are graphed in three dimensions in Figs. 15 and 16 respectively. In the graphs for all species there is a trend from a central core composed of comparatively high values to an outer periphery, somewhat spherical in shape, composed of very low values. For each individual species, this central core is situated within a specific portion of the total volume representing the environmental limits of the study. This position is different for all species and seems to be situated independently of those of all other species. Similarly the amplitudes of tolerance differ in both size and shape for all species, with no groups occupying identical situations.

The distribution for any species may be the resultant of a combination of environmental factors and present a true picture or it may be due to an inadequate resolution of these factors in the ordination itself and thereby deviate from a spherically symmetrical distribution, just as the bimodal nature of species curves on the linear gradient is a distortion of the normal curve representing a species amplitude, due to failure to select the important controlling factors. The effects of this distortion may be understood by careful examination of the 3 separate sheets for a species. They present a view of the species pattern from 3 angles, and in at least one of the graphs, the pattern tends to appear more compact than on others. This may be indicative of a greater controlling influence exerted by the factor represented in the particular axis in question.

In Figure 17 the distributions of importance values of 100+ for *Abies balsamea*, *Picea glauca*, *Pinus strobus*, *Thuja occidentalis*, *Acer saccharum* and *Tsuga canadensis* have been graphed and lines connect these stand positions. Thus the somewhat spherical patterns in the 3 graphs can be considered as the 100+ importance value isolines for each species. All the stands within each pattern often have as high an importance value but all necessarily do not, since any one of the stands might be distantly separated in the dimension not accounted for in any single presentation. Several points are noteworthy in these presentations. Note that each species occupies a specific place in the gradient, although the amplitudes of individual species vary. Notice that *Picea glauca* and *Pinus strobus* occur usually at opposite ends of the graph from *Abies balsamea* and *Thuja occidentalis* and especially so in the primary-secondary axes graph which is considered to separate

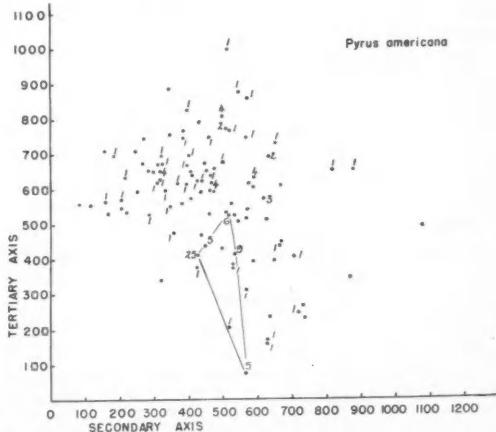
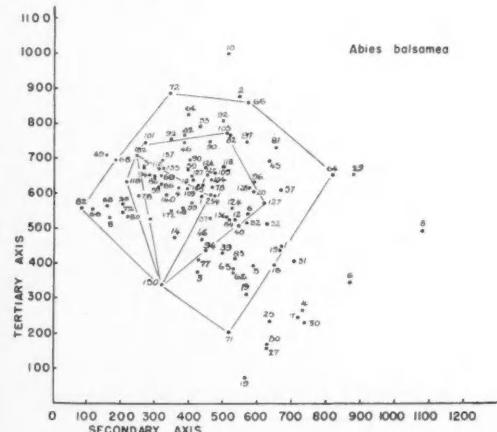
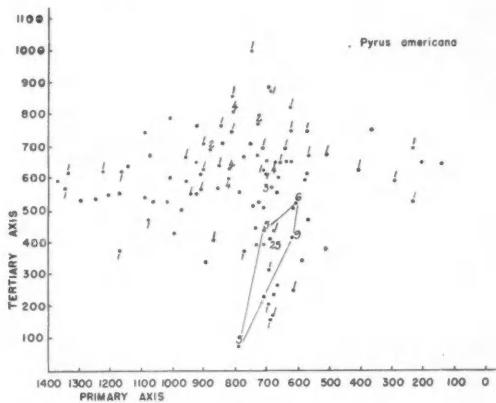
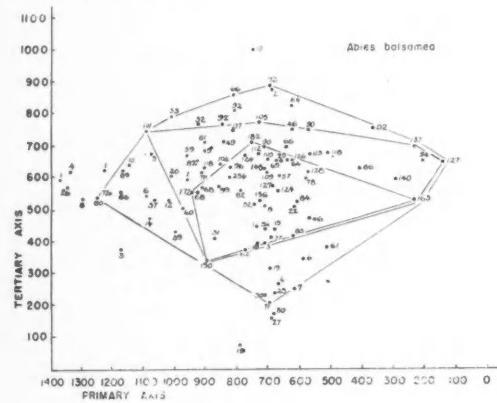
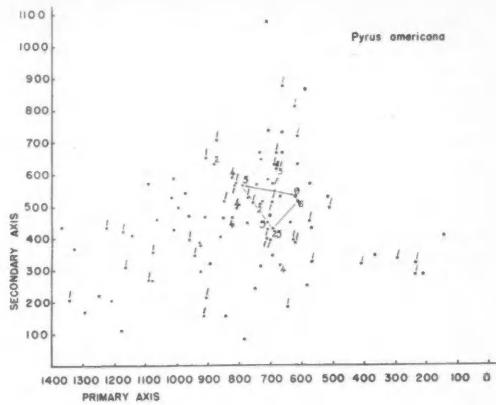
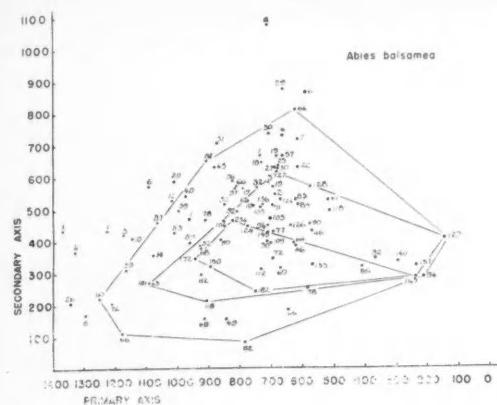


FIG. 15. The distribution of importance values for *Abies balsamea*, two dimensions at a time, as derived in the three-dimensional gradient. The space on a page limits the presentation of species patterns to two dimensions at one time. Thus each axis is represented twice rather than a single time in the above presentation, but the axis in question is always identical. Thus the primary axis of the lowermost section of the figure is duplicated in the middle section. The 3 sections of the figure, when viewed in order from bottom to top, provide an

impression of the distribution of importance values for *Abies balsamea* in 3 dimensions. The spherical patterns have resulted from joining the series of values most distant from the center of action, of 150+, 100+ and 50+ to form isolines. The vertical order of figure sections has no special significance.

FIG. 16. The distribution of *Pyrus americana* in consecutive two-dimensional graphs which show the dispersion of the importance of this tree in the three-dimensional ordination. Thus the three separate sections of

ecologically dry and wet habitats. Notice that *Acer saccharum* and *Tsuga canadensis* occur between the aforementioned groups. Apart from these separations it may be noted that all these distributions intergrade and that they defy any attempts to segregate them into types in a single dimension let alone all three. Finally mark the fact that the distribution for *Abies balsamea* is of a greater extent than any of the others at this level of importance and thus it knits the associated members together. To this species belongs the potentialities of conferring the aspect of a community to the vegetation of the northern Great Lakes region, now considered.

Such patterns not only exist for these top-ranking members of the community but are also shown by less important tree species as illustrated in Fig. 18. The previous comments apply equally as well in this situation where importance value isolines of 5+ form the basis for species distributional patterns. These isolines, as did the previous, delimit the situations of optimum development for each particular species in the ordination. In Fig. 17 as in Fig. 18, the intergrading spherical patterns are again evident and the whole environmental complex is occupied by a mosaic of species distributions, each tending to find optimum conditions in a specific situation. The intersecting patterns preclude the possibility of compartmentalizing species into distinct community units.

The continuous nature of the community and the distinct relationships of species components is further displayed in Fig. 19 in which the center points of the behaviors as indicated by importance values, for a majority of the tree species are presented in three-dimensional relationship. The center points on each axis were determined by graphing the importance values at a level of significance and then selecting the midpoint in each dimension. The central points of individual species on each axis are presented in Table 7.

One useful purpose served by the dimensional treatment is illustrated in the graphs for *Picea mariana* (Fig. 20). When plotted on the primary and secondary, and primary and tertiary axes, two definitely separated centers of high values are evident. On the secondary and tertiary axes, a spherical distribution with a core of high values results. These same patterns can be better seen in the photographs illustrating the distribution of *Picea mariana* on the three-dimensional model. When viewed at an angle perpendicular to the primary axis (Fig. 21), the two separated groups of large beads representing higher importance values are visible. These groups would produce a bowl-shaped distribution if averaging

the figure, when viewed in order, present a picture of the distribution of importance values in three dimensions, two dimensions at a time. The isoline of 5+ values is indicated. Note that although the species was recorded as only present (value 1) in many stands distributed over the entire gradient, the values greater than one are confined to relatively isolated portions. This species was not employed in the ordination technique. The vertical order of figure sections has no special significance.

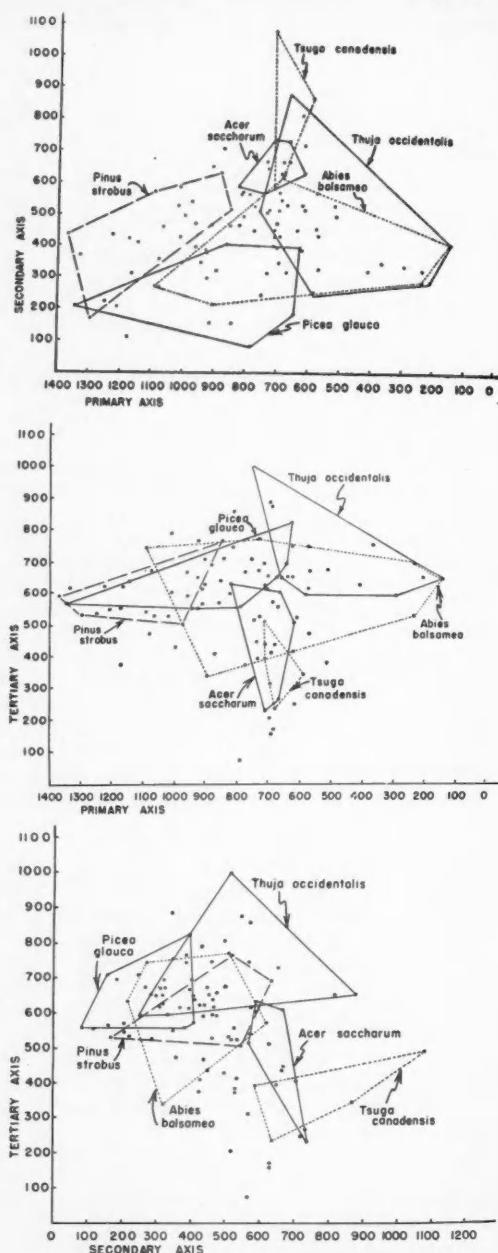


FIG. 17. Isolines representing importance values of 100+ for major tree species. The three sections of the figure, representing two-dimensional aspects of a three-dimensional distribution pattern, provide an indication of this pattern when observed in relation to each other. Each tree species occupies an isolated segment of the three-dimensional gradient. Note that the distribution of *Abies balsamea* tends to enclose the distributions of a majority of the other species and is responsible for the semblance of phytosociologic unity of the community.

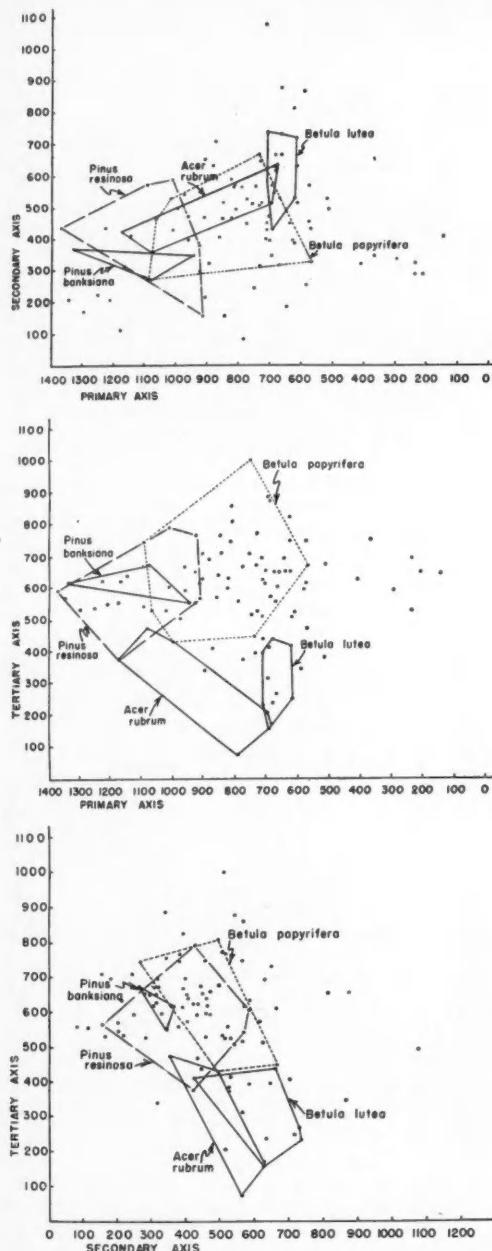


FIG. 18. The 50+ importance value isolines for additional tree species in the three-dimensional gradient, presented two dimensions at a time. Each species tends to find its optimum distribution in a particular portion of the gradient but the intergradation of species distributions is an indicator of the continuity of the entire community complex. The order of figure sections is of no special significance since each when viewed in relation to the others provides an indication of the three dimensional aspects of the distributions.

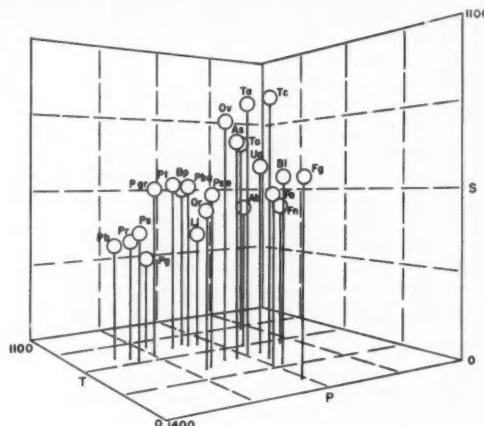


FIG. 19. The locations of central points of species behavior as indicated by importance values, presented in three-dimensional aspect. The determination of midpoints is presented in the text, and the species abbreviations are provided in Table 7.

TABLE 7. Location of midpoints of tree species on the three ordination axes. Midpoints represent mean axis locations of importance values and define the centre of influence of species in terms of the sum of relative density, relative dominance and relative frequency.

	P	S	T
<i>Pinus strobus</i> (Ps).....	1125	400	630
<i>Picea glauca</i> (Pg).....	975	250	685
<i>Abies balsamea</i> (Ab).....	600	410	560
<i>Thuja occidentalis</i> (To).....	450	565	800
<i>Tsuga canadensis</i> (Te).....	660	800	400
<i>Acer saccharum</i> (As).....	725	660	425
<i>Fraxinus nigra</i> (Fn).....	440	390	525
<i>Pinus banksiana</i> (Pb).....	1200	325	650
<i>Ulmus americana</i> (Ua).....	630	575	450
<i>Pyrus americana</i> (Pa).....	700	510	300
<i>Prunus serotina</i> (Pse).....	925	515	410
<i>Prunus pensylvanica</i>	700	500	425
<i>Quercus rubra</i> (Qr).....	940	475	365
<i>Tilia americana</i> (Ta).....	675	765	460
<i>Pinus resinosa</i> (Pr).....	1140	370	575
<i>Betula papyrifera</i> (Bp).....	830	460	710
<i>Populus tremuloides</i> (Pt).....	900	500	660
<i>Betula lutea</i> (Bl).....	660	575	325
<i>Fraxinus americana</i>	630	575	440
<i>Fagus grandifolia</i> (Fg).....	730	600	125
<i>Ostrya virginiana</i> (Ov).....	840	725	420
<i>Larix laricina</i> (Ll).....	765	315	660
<i>Populus grandidentata</i> (Pgr).....	1040	500	630
<i>Populus balsamifera</i> (Pba).....	830	470	675
<i>Acer spicatum</i>	720	620	525
<i>Acer rubrum</i>	925	500	270

techniques were performed along this axis. When the model is rotated 90° and viewed from above (Fig. 22), only one compact grouping with central high values is visible. This would indicate that other factors influence the distribution of *Picea mariana* and moisture conditions of site are less significant. A majority of the other bowl-shaped and bimodal distributions of other species on the original moisture

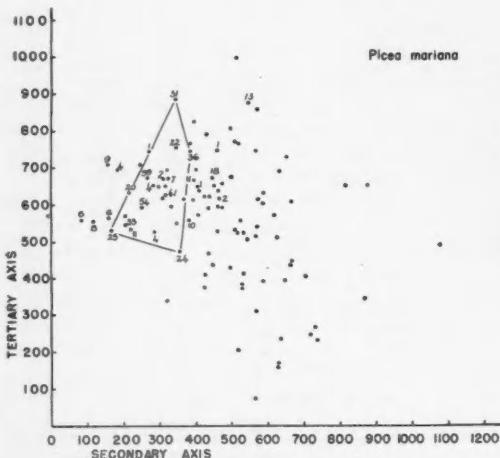
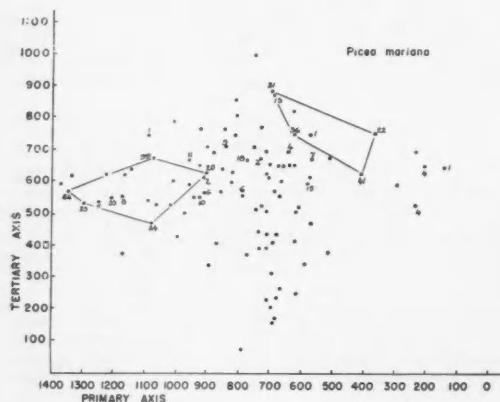
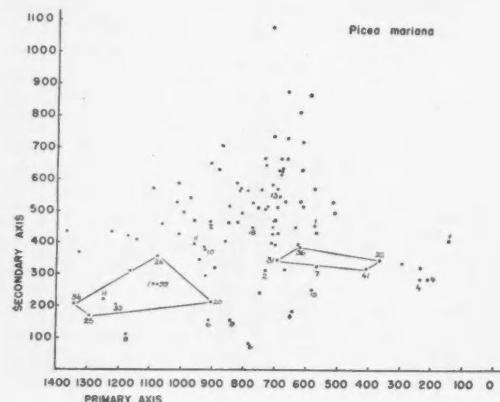


FIG. 20. Importance values for *Picea mariana* plotted in the dimensional ordination. Values of 20+ are connected by lines. When viewed toward the primary axis two groups of high values are evident. On a linear gradient this separation produces a bowl-shaped curve indicating the species attains optimum development in both dry and wet conditions of moisture. When viewed

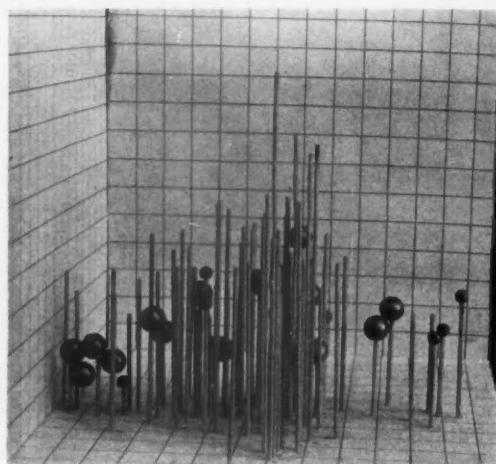


FIG. 21. A three-dimensional model which presents the spatial relationships of the 102 stands to each other. Balls represent the distribution of importance values for *Picea mariana*, the large—importance values greater than 10, the small—less than 10. Note a separation of large balls into 2 groups to the right and left. The model is viewed toward the primary axis.

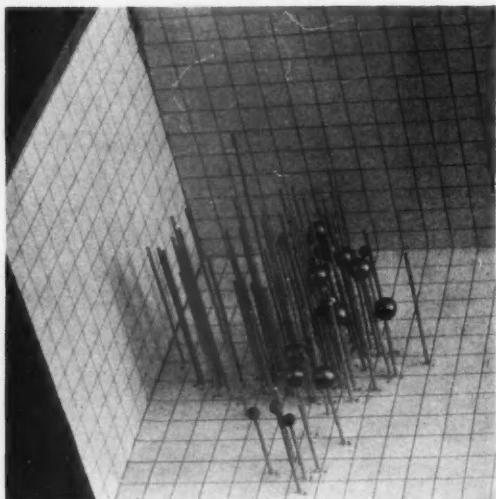


FIG. 22. View of the same model as in Fig. 21 but with the model rotated 90° so that one is facing the tertiary axis and looking down from above in the general direction of the secondary axis. Of special ecological significance is the fact that all balls representing the occurrence of importance values are confined to a relatively narrow portion of the tertiary axis and are grouped in a straight band from the side of the model adjacent to the viewer to the opposite side. When viewed thus, the bowl type of distribution evident along the primary axis (Fig. 21) assumes the typical normal type.

toward the secondary and tertiary axes, however, a spiral pattern is evident, indicating the importance of some other factor than moisture as a controlling influence.

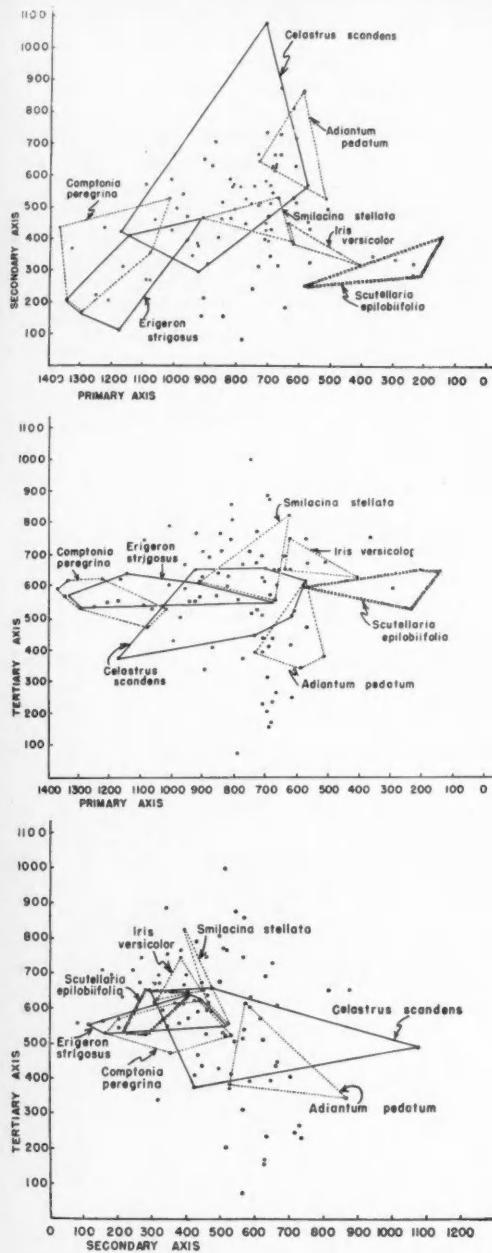


FIG. 23. The distributions of a group of herbaceous species of minor importance, none of which were used in the construction of the three-dimensional ordination. The 3 sections of the figure convey the three-dimensional aspect of species distributions when viewed in relation to each other, although each represents only a two-dimensional view. Note that in each presentation, each species attains optimum importance in an isolated portion of the gradient, yet all species intergrade. Stands of occurrence are either connected or enclosed by the lines.

gradient were resolved in a similar manner. These discrepancies disappear in at least one of the axes and such circumstances go far to indicate the limitations of single factor environmental treatments. These examples should serve as a warning to the investigator who holds the opinion that environmental requirements of species may be ascertained by casual field observations.

The relations of various herbaceous and shrub species to the ordination follow the same general patterns as the tree species. Many of their distributions have been tested and all produce atmospheric distributions of the type mentioned above. Groups of species could be separated and arbitrarily grouped together on the basis of their activities on any of the three axes. These relationships hold true not only for the group of species used in the ordination process but also for species of very minor occurrence. Proof of this point appears in Fig. 23 in which the patterns for species with low percent presence values are presented. The patterns result from joining stands in which the species in question was recorded as present. *Adiantum pedatum* was present in only 4 stands of the 102 represented, *Smilacina stellata* in 5 and *Iris versicolor* in 3 but in every instance the stands of occurrence for these species lie remarkably near one another. These species were not selected for this purpose but were chosen at random from a large group with low percent presence values, any of which would have been as suitable to show the patterns illustrated. Of these minor species, note that each finds its optimum in a particular segment of the gradient.

Of the 3 species of *Smilacina* present in the stands studied, only *S. racemosa* was used in the ordination itself, yet in Fig. 24 where the presence patterns are displayed, it is evident that each species tends to find optimum conditions for growth and

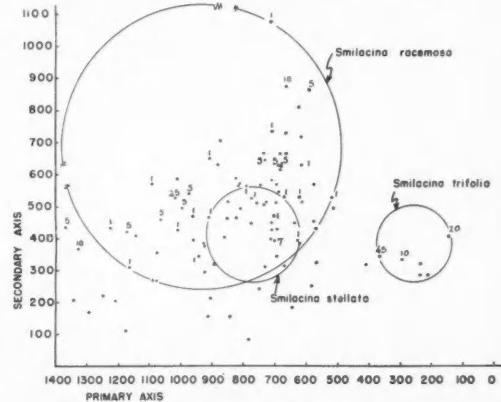


FIG. 24. A partial three-dimensional presentation (primary-secondary axes) of the distributions of 3 separate and taxonomically distinct species of the genus *Smilacina*. Those stands in which the particular species was recorded as present are enclosed. The figure clearly indicates that ecological distinction supports taxonomic separation.

development in a particular range of the environment. A clearly defined separation of ecological behavior is displayed. This is analogous to the situation presented for species of the genus *Goodyera* on the moisture gradient except that in this instance, distributions are represented in three dimensions.

When the distributions of widespread species, as for example *Maianthemum canadense*, *Aralia nudicaulis*, *Aster macrophyllus* and *Cornus canadensis*, are plotted on the gradient their patterns indicate a very broad ecological tolerance and in most instances their patterns tend to pass beyond the limits of the gradient itself. Higher values are however closely grouped together on the gradient and the distributions point to the fact that these plants are important in vegetational types related to the mixed boreal conifer-hardwoods. This is of course borne out by the fact that the examples mentioned pass far north into the true boreal forest and occur as important community components in the related and more southerly distributed northern conifer-hardwoods.

Because space does not permit an exhaustive treatment of plant species in relation to the gradient, an attempt has been made to portray relationships which are representative of the more important ecological types. In general all species tend to show the same type of pattern. If the distributions of all species could be placed on one great model without confusion, a group of intersecting spheres would result. Such would be expected of all species which form an integral part of one continuous community complex. If it does nothing else, this treatment points to the fact that only a start has been made in attempts to understand the complex interrelationships of species comprising vegetation. The problems of the basis for community structure, the relations of species, and the integration of plant communities will never be fully answered in terms of distinct community units, in the light of the present findings.

ENVIRONMENTAL FACTORS AND THE ORDINATION

The remarkable similarity displayed by the distributions of quantitative values for species in both the moisture gradient treatment and the multi-dimensional ordination, coupled with the similarity of the original moisture class assigned and the relationships of these assigned classes on the multi-dimensional gradient (Fig. 14), confirms the fact that the primary axis is predominantly one of moisture. The most unlike stands of the entire assemblage are different because of moisture characteristics. Thus as would be expected, when moisture retaining capacity values are plotted on the dimensional ordination, low values are concentrated at the lower end of the primary axis and higher values at the opposite end, and a gradual transition occurs along the length of the axis. There seems little doubt that light is also an important environmental influence along this primary axis with a tendency for light values to be higher in the open stands of the lower end, lower in the mesic stands of the central portion and very low in the close-canopied cedar swamps at the upper end. The

influence of light is not, however, so simple since there is little doubt that light relationships are interwoven with other important environmental influences along the secondary axis.

In respect to the secondary axis, the distributions of the dominant tree species shed as much light upon its significance as any of the environmental factors. Fig. 19 indicates that all coniferous species with the exception of *Tsuga canadensis* and *Thuja occidentalis*, find their center of influence at the lower end of the secondary axis, whereas deciduous species in general attain their centers of influence higher up on the same axis. This would seem to infer that the secondary axis is related to succession and/or disturbance. The pioneer species, *Populus tremuloides*, *P. grandidentata* and *Betula papyrifera* are adjacent to the conifers, inferring further a trend from early successional stages to more stable communities along the secondary axis. For this reason it is also apparent that other environmental factors are also closely connected with the secondary axis and light and the type of litter or leaf fall are no doubt among the important ones. In this connection a comparison might be drawn between the litter types found in stands composed predominantly of *Fagus grandifolia* which produces a litter resistant to rapid decay when compared with that produced by *Acer* and *Tilia*, and the types of litter in open *Pinus strobus*, *P. resinosa*, *Picea glauca* and *Abies balsamea* stands. Although these types are markedly different, their effects on the habitat may tend to produce a type of ground layer similar enough to draw them closely together on the secondary axis although the centers of importance of these species are widely separated on the primary axis. That *Tsuga* seems to respond similarly to the mesic deciduous species of *Acer* and *Tilia* should support the contention of the late J. E. Potzger concerning climax in the Lake Forest of Weaver & Clements. ". . . the writer does not agree that all climax dominants must belong to the same sub-phylum. If *Tsuga* was the mesophytic representative of the Gymnosperms, I see no reason why it should not become a codominant in a mesophytic forest complex constituted primarily by Angiosperms." (Potzger 1946).

DISCUSSION

An attempt has been made in this study to assemble quantitative data for a wide variety of vegetational types, selected as objectively as possible, and then to delimit species relationships in the absence of preconceived ideas of community structure, or associational vegetation units. Before discussing these results in relation to community structure and dynamics as well as to the findings of others, a few of the broad conclusions reached may be considered.

Two major treatments have been attempted. The first was based on the moisture relations of site and therefore assumed a controlling effect of moisture on community development. This approach was of necessity somewhat less than entirely objective, in large measure due to the inability to provide a single

index to encompass the effects of moisture of site, independent of vegetation.

The second of the methods was completely objective, with the quantitative data for a large group of component species acting as the sole determiners of the resulting patterns obtained. The remarkable similarity of the results of both these procedures, and the fact that the latter supported and extended the findings of the former, is evidence to support the application of either. The multidimensional ordination provides a means to a more precise determination of the ecologic sphere of action of any species in relation to the entire community complex.

In the results of both of these presentations, the continuous aspects of the boreal and boreal conifer-hardwood vegetation in the Great Lakes region is clearly indicated. Those species critically examined tended to occupy a specific portion of the linear moisture gradient, or possessed a limited sphere of action within the three-dimensional presentation. Both of these patterns of ecologic tolerance are so inseparably related that a species pattern on the moisture gradient may be superimposed upon its pattern in the three-dimensional complex, without effecting perceivable changes.

While it was found that no single species tended to occupy positions in either situation to the exclusion of all others, it is also true that no group of species occupied a center of action to the exclusion of all other groups. Such arrangements defy all attempts to segregate distinct associations of species. Fig. 19, displaying the centers of action of tree species on the multi-dimensional ordination, is convincing evidence of the futility of such attempts.

All species play integral roles in an extensive community complex which can be considered to exist in both time and space. These species are arranged in an orderly but independent manner along a series of environmental gradients which tend to converge upon a situation somewhat representative of mature conditions of a mesic nature, presenting an environmental complex of moderate moisture, low light and high amounts of incorporated organic matter. This situation is gradually displaced by conditions of increased moisture, less light and higher accumulations of organic matter in one direction; and in another by conditions of relatively decreased moisture, abundant light and impoverished amounts of incorporated organic matter. These relationships result in a three-sided environmental pattern. This situation bears no direct or linear relationship to successional tendencies but succession undoubtedly is an active agent in the complex.

The entire assemblage of species can be said to represent a vegetational continuum, in which all species interact and position themselves in environmental situations most suited to their continued existence. Effects produced by or resulting from the interactions of species themselves are probably as influential as any separate or combined environmental factors, which similarly fluctuate in gradational series. This continuum may be represented in multi-dimensional

patterns and the factors controlling its existence may perhaps be similarly resolved. These relationships must be of major consideration in any interpretation of other community aspects or in any treatment performed for a variety of theoretical or practical purposes.

RELATED APPROACHES

There has recently occurred an increase in the use of quantitative methods in phytosociology. When data are objectively obtained for a wide variety of vegetational types, without regard to successional relationships or preconceived notions of community structure, they offer one of the strongest supports for the continuous nature of vegetation. These conceptions are in defiance of distinct associations and community entities and have developed progressively on this continent since the appearance of Gleason's 1926 paper on the individualistic nature of plant communities. Brown & Curtis (1952) and McIntosh (1958) review many of the papers favoring the continuum approach, but several papers dealing with boreal forest types are pertinent to the present study.

Whittaker (1951, 1952, 1956) in the Great Smoky Mountains, encountered a continuous sequence of vegetation types related to an environmental series from mesic to xeric conditions, at both lower and higher elevations. In the spruce-fir forests composed of *Picea rubens* and *Abies fraseri*, only a limited difference in canopy composition was exhibited, but a striking variety of understories related to site moisture, was evident. An analogous situation prevails in a similar community in the Lakes region. Stands of very similar tree composition in different moisture situations often display great differences in under-story composition and structure. On the other hand, a number of herbaceous and shrub species are capable of tolerating a broad range of moisture conditions and tend to link these various phases of the community together into an integrated whole. Whittaker preferred to interpret vegetation as a complex and continuous population pattern.

In the boreal mixedwood region in southern Manitoba and Saskatchewan, Rowe (1956) conducted a study of forest vegetation while attempting to develop a method of describing stands for forestry purposes. In this district there were only 8 tree species: *Picea glauca*, *P. mariana*, *Pinus banksiana*, *Abies balsamea*, *Larix laricina*, *Populus tremuloides*, *P. balsamifera* and *Betula papyrifera*, all of which grow throughout the Great Lakes region. Rowe's analysis indicated that various combinations of these species gave rise to a large number of cover types. General observations had indicated a relation between these types and soil moisture and stands were grouped into 5 moisture classes of dry, fresh, moist, very moist and wet. The presence of trees, shrubs and herbs was tallied in stands of these segments to determine their relationships to the moisture series. Most of the trees possessed wide ranges of tolerance along the moisture series and thus were of little use in characterizing stands as was also true of a group

of widespread herbaceous species. Other plants showed preferences for particular moisture segments but in most instances they were seldom strictly confined by water relationships. That the vegetation exhibited the aspects of a continuous pattern and did not permit the recognition of distinct types was summed up by Rowe as follows:

"The position of each species relative to the moisture preference scale is not meant to be interpreted in a hard and fast way. Plants of wide tolerance may be found in all sorts of communities from dry to wet sites. However most of the species exhibit a preference for one moisture regime (their optimum) over others, reflecting this preference in greater abundance and vigor."

This investigation by Rowe has been reviewed in detail because of its remarkable similarities to the present investigation. The studies were conducted independently but the treatments and results are similar. Rowe listed 200 species, 140 of which were also sampled in the Great Lakes region. Although the moisture gradient established for Manitoba and Saskatchewan covered a broader range of moisture, the same species were characteristic of the same or similar moisture segments. Many of the widespread species were identical and of equally poor value as site moisture indicators. A gradational series of vegetation types composed of integrated species with overlapping environmental tolerances was the interpretation in both situations. Finally a vegetational moisture index, assigned to each stand by weighting species of occurrence, relative to their optimum position on the moisture scale, resembled somewhat the herbaceous indicator technique applied in the present work. This illustrates that investigators may arrive at similar results and conclusions in widely separated regions in related vegetational communities, when approaches remain objective. The results of these studies may be integrated to obtain a more complete picture of the total boreal vegetation complex.

In the related forests in the foothills of the Rocky Mountains in Alberta, Horton (1954) found the continuum concept was equally applicable.

Fraser (1954) studied tree composition as related to soil moisture in an upland mixed conifer-hardwood forest at Chalk River, Ontario. Tree species usually were found to occupy a comparatively broad range on the moisture series and understory associates appeared to be more restricted by water relations. A graph presenting the overlapping tolerances of trees on the moisture gradient resembles the results of the present study and favors the continuous aspects of vegetation.

The lowland conifer bogs of Wisconsin, which in terms of composition are closely related to stands at the wet end of the moisture gradient, were investigated by Clausen (1957). These forest types, comparatively more simple in terms of tree composition, were found to produce similar patterns along the compositional gradient established, and indicate that

both studies may be integrated to provide a broader picture of boreal species relationships over a wider range of moisture conditions.

The close relationships to the upland conifer-hardwood forests in northern Wisconsin (Brown & Curtis 1952) have already been commented upon. The similarities of stands of the central mesic portion of the moisture gradient to the terminal mesic segments of their upland continuum is also of significance. Since the terminal forests in the northern parts of the state were in turn related to the terminal hardwood stands in Southern Wisconsin (Curtis & McIntosh 1951), the ultimate integration of all three forest types into one great and continuous forest complex is foreshadowed. The multi-dimensional treatment of Bray & Curtis (1957) for these southern forests is so similar in method and approach to the present study and provides such coinciding results, that it goes far to corroborate this conclusion.

STATUS OF THE NORTHERN GREAT LAKES FORESTS

The present study certainly indicates that any interpretations of the forests of the Great Lakes region must be in terms of the Boreal and Deciduous forests and the component species of both. These forests have been considered to exist as a distinct unit (Weaver & Clements 1929), as a northern portion of the Deciduous forest proper (Nichols 1935; Braun 1950), and as an ecotone or tension zone between the Boreal forest to the north and the Deciduous forest to the south (Nichols 1935; Braun 1950; Dansereau 1943). Braun (1950) has claimed that a mingling of species occurs in the ecotone whereas Dansereau (1944) believes that it is actually a mixing of distinct associations yet both favor the concept of interpenetrating climax. To favor the ecotone approach is to recognize that both the Boreal and Deciduous forests are composed of distinct associations.

Many of these approaches have been based on the assumption that certain forest types are climax and terminal in the area. Quantitative data for 103 stands in the present study fail to indicate that *Picea glauca* and *Abies balsamea* reach their optimum development in the most mesic sites available. To the contrary these species indicate completely different relationships, with *Picea* attaining optimum development on the dry sites and *Abies* in the wet situations. Their broad range of tolerance to moisture conditions, apart from conditions suitable for optimum development, may influence their being considered as mesophytic species. Neither species reproduces successfully in the dense shade of any forest cover, especially their own. In stands where reproduction appeared to be successful, disturbance was or had been active, often caused by the death of older members of the canopy, by wind thinning and in a few locations by light infestations of budworm. Both *Picea* and *Abies* reproduce profusely in open situations on exposed mineral soil, and fallen logs provided a suitable seedbed. Often saplings which had established themselves on rotting logs succumbed, apparently from

suppression. The presence of large specimens of *Picea* and *Abies* often prompted an examination of ages and trunk bases. Very often these specimens were younger than the hardwoods; and the rotting log at the base indicated establishment on logs in openings as in gap-phase replacement. *Betula lutea* and *Tsuga canadensis* acted similarly.

In the southern areas, mature *Picea* and *Abies* were usually sparsely scattered through hardwood stands, but in more northern sections, especially on rocky deposits with deep humus accumulation, continuous minor and local disturbances, maintained these species as a noticeable portion of mixed stands. In general it was evident that in boreal conifer-hardwood mixtures, there was a trend toward the development of a pure hardwood canopy, as indicated by saplings, and the attainment of such composition was dependent upon the relative amount of disturbance. *Acer saccharum* and *Betula lutea* grow successfully throughout the area as well as most other hardwoods, and their tolerance curves indicate they attain optimum development on mesic sites.

If some general statement concerning the ultimate terminal forests of the area should be made, the mesophytic forests composed predominantly of hardwood species should be favored. If this is described as the climax it must be recognized that it is probably more hypothetical than real. In northern regions the question of terminal climax becomes highly doubtful, since large scale catastrophe is prevalent and prevents the termination of succession. The hypothetical climax has little meaning in areas continually subjected to fire, windthrow and budworm infestation. These and other disturbances cause a reversion of successional development and permit the continuous entrance of species suited to such conditions. Throughout the Great Lakes area and northward, *Picea* and *Abies* certainly represent such species. It must be recognized that this question of climax is a separate and distinct consideration. It should not and cannot prevent the investigation of community structure and species relationships and it certainly should not be permitted to replace them.

To provide an answer to the problem of the relative status of the Great Lakes forests we need only consider the relations of the many species which collectively result in their structure. The curves representing ecological tolerances form a reliable basis for interpreting the nature of forest relationships.

If plants are confined in their distributions to distinct associations there should be a similar grouping of their environmental tolerances with little or no overlapping, on a gradient of environmental factors. If associations are fairly distinct but permit broad ecotones of vegetation which are only partially similar to the associations they are derived from, then groups of species with similar tolerances with noticeable overlapping should be fairly evident.

In the present study when the environmental relationships of species were determined by two objective procedures, no groups of species tolerance curves were confined to specific areas on the environmental

gradients, in fact it is probably true that no two species indicated exactly similar relationships. Not even partial groupings were in evidence, but a continuous series of intergrading and overlapping amplitudes of tolerance resulted. Thus, if one persists in attempting to categorize vegetational types only two treatments are possible, either the indiscriminate lumping of diverse types or the establishment of a large number of unruly associations. Either treatment will defeat the intended advantages of classifying. The most reasonable alternative would be to treat continuous phenomena in a fashion which recognizes the continuity and yet permits a segregation for theoretical and practical purposes. Both the moisture gradient and multi-dimensional treatments attempted permit this desired result. While communities have not been classified, the optimum situations for development have been somewhat localized in various segments of the vegetational gradient which will facilitate autecological investigations and the eventual integration with other vegetational communities.

Thus the forests of the Great Lakes region are not a distinct associational unit. They do not collectively comprise an ecotone between two completely separate community types. They can best be considered as a portion of a vegetational gradient representing a part of a vegetational complex which in the southern areas of the Great Lakes region is composed entirely of broadleaf tree species and in the areas northward becomes predominantly needle-leaved in character. Similarly a gradual replacement of understory associates takes place with greater proportions of boreal representatives northward. To imply that any one of the many possible phases of community structure is either distinctly of one type or the other, or possesses a nature entirely its own, is to refute this continuous nature.

SUMMARY

Quantitative data of tree and herbaceous composition were collected for 110 upland forest stands selected on the basis of boreal relationships, throughout the Great Lakes region from Minnesota to Ontario. Only stands free from disturbance in the lifetime of the existing trees and of at least 15 acres in size, were sampled by the quarter method.

Relative frequency, relative density and relative dominance were calculated for all tree species in all stands. These 3 relative values were summed to provide an importance value. Frequencies were determined for all herbs and shrubs on the basis of their occurrence in meter square quadrats.

Two major treatments were attempted. The first assumed the controlling effect of site moisture on plant relationships. Stands were segregated into 5 broad moisture categories from dry to mesic to wet, with two intermediate groups, and the quantitative measurements available were averaged for each segment of the moisture gradient. When these averages were plotted they usually formed smooth normal

curves, representing the ecological tolerances of species to moisture conditions. The peaks of these curves corresponded with the situations of optimum development.

The second treatment can be considered purely phytosociological in that only the quantitative aspects of species themselves were employed in placing the stands in spatial relationship to each other. A three-dimensional ordination was constructed by comparing the quantitative values of a group of selected species for each stand with those of every other stand to obtain values which were employed in positioning stands along a series of axes on the basis of their floristic similarities and dissimilarities. The 3 axes were resolved by choosing the most unlike stands as indicated by the comparison values, and using these as the ends of the primary axis. Secondary and tertiary axes were then determined by selecting the most different pair of central stands on the preceding axis and using these as the ends of the axis in question. In this manner a spatial arrangement of stands in three dimensions was produced with the proximity of a stand to its neighbors determined on the basis of floristic similarity. Quantitative values for community components could then be plotted graphically in series two dimensions at a time, or represented structurally on a three-dimensional model. Species occurrences in this presentation could be described as solid spheres, occupying a specific range of environmental conditions, with high values centrally aggregated and values decreasing toward the periphery.

The total assemblage of species on the moisture gradient resembled an intergrading series of normal curves with no two species possessing identical amplitudes of tolerance. In the dimensional treatment the situation resembled a group of intersecting spheres, each with independently determined positions and yet interrelated. Again, while it was found that no species occupied a position to the exclusion of all others, it was also true that no group of species was distinct in respect to the ecological tolerances of its members.

Each treatment supported the results of the other and both offer strong evidence in support of the continuous nature of the forests of the Lake region.

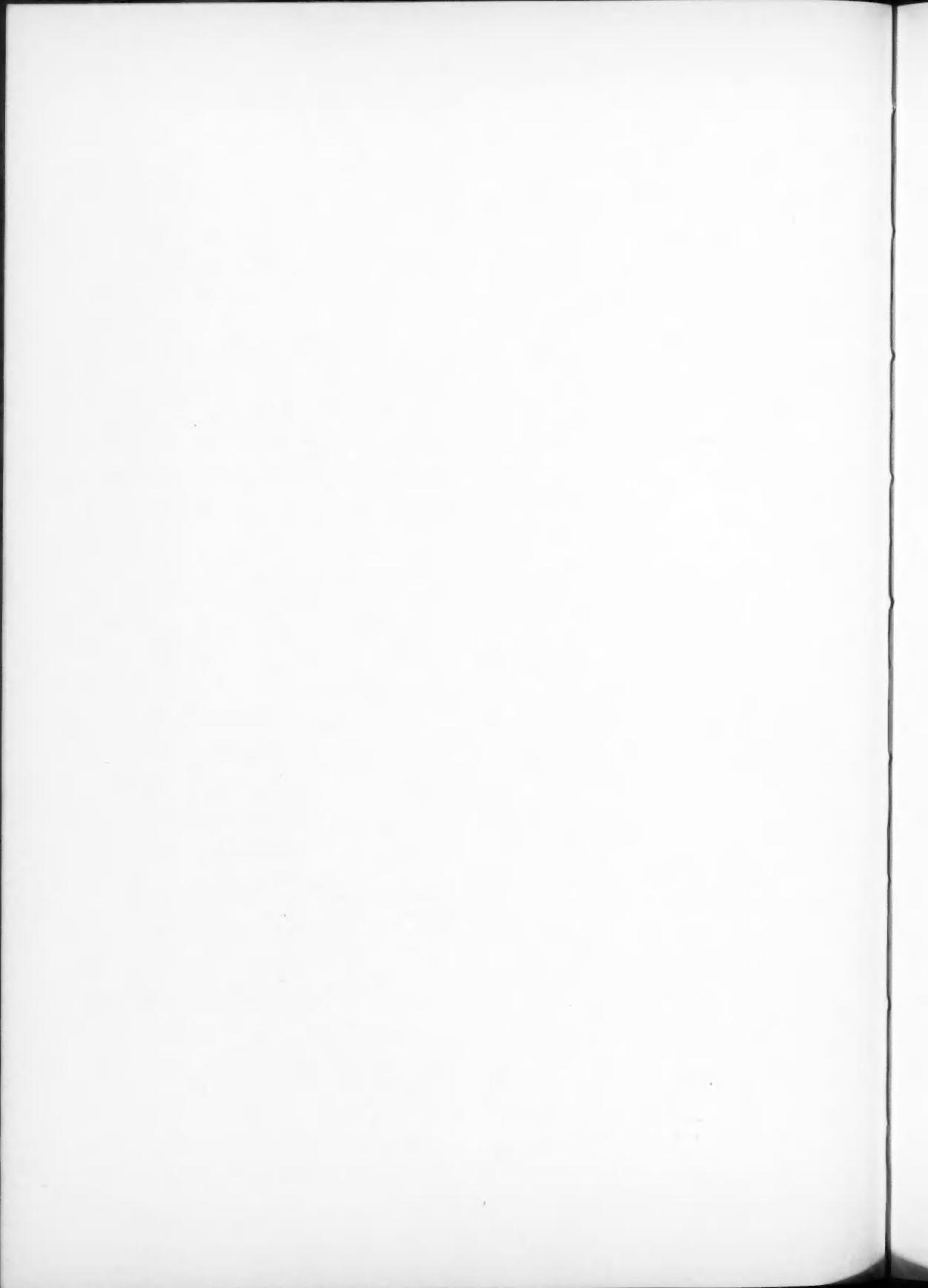
Any interpretations of the nature and status of these forests must be based on the ecological tolerances of the component species which are also important in related and neighboring forest communities. A gradually changing environmental complex northward results in gradually changing floristic composition toward greater representation by boreal species. To imply that any particular community is either representative of the Boreal or Deciduous forest or that it possesses characteristics entirely its own, is to refute its continuous nature in terms of this floristic composition and the ecological relations of its component species.

These forests of the Lake region are considered to form a vegetational continuum and to be inseparably related to all neighboring vegetational types.

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FLOOD PLAIN VEGETATION OF THE CENTRAL MISSOURI VALLEY AND CONTACTS OF WOODLAND WITH PRAIRIE

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INTRODUCTION

The Missouri River, like some of its great tributaries, rises high in the Rocky Mountains. With thousands of tributary streams it drains the water from plains and prairie to form a mighty river with a flood plain many miles wide. It has made a bluff-rimmed depression and numerous tributaries and their branches have cut canyons below the general level of the wind-swept grasslands. Its main tributaries from the west—the Niobrara, Elkhorn, Platte, and Big Blue—flow east or southeastward. The Big Sioux River bordering Iowa, enters the Missouri from the north, and large tributaries in Iowa—the Little Sioux, Boyer, Nishnabotna, Tarkio and Nodaway—flow more southward than westward (Fig. 1). The Missouri River separates southeastern South Dakota, Iowa, and a part of Missouri from Nebraska. So profoundly has this river modified the effects of the general grassland climate that in many places prairie has given way to woodland and forest.

Several distinct forest communities along the river in southeastern Nebraska and adjacent parts of Kansas, Missouri, and Iowa extend for short distances over the uplands, but farther along the major streams. Most of the trees and shrubs of this forest are near the extreme western limit of their range. The extreme outposts of the forest are represented by relatively few species of trees and shrubs along the creeks and sheltered ravines which more or less dissect the hilly and rolling portions of the prairie.

With these the grassland had immediate contact over many thousands of miles.

The several belts of forest communities on the river bluffs and adjacent hills are, beginning with the most mesic, red oak-linden (*Quercus borealis maxima* and *Tilia americana*), black oak-shellbark hickory (*Quercus velutina* and *Carya ovata*), and bur oak-bitternut hickory (*Quercus macrocarpa* and *Carya cordiformis*).

The bur oak community is usually but not always bordered by a more or less continuous community of shrubs which separate it from prairie. Northward beyond the mouth of the Platte the more mesic forest communities almost disappear. There is a decrease in the general area occupied by woody vegetation, decrease in number of species, dwarfing in size of individuals, and trees are confined to the more favorable sites. Conversely, the area covered by shrubs greatly increases.

Tongues of woodland follow up the stream courses into Iowa northeastward to the Missouri-Mississippi divide, and far into Nebraska and northern Kansas westward. Such belts of timber vary from a few yards in width at the stream sources in grassland to 0.5 mi or more along their lower limits where they merge insensibly into the main body of timber on the Missouri River bluffs and along the valleys.

The area of this study is approximately 50,000 sq mi. It includes the portion of the Missouri Valley in western Iowa, eastern Nebraska and parts of the 3 adjoining states. Forested areas in the Missouri



FIG. 1. Central part of the Missouri River and its tributaries.

Valley drainage of western Iowa are less abundant than those west of the river. In southeastern Nebraska the average width of the general potential forest area is, according to Aikman (1929), about 15 mi; in the vicinity of Omaha it is about 5, but in northeastern Nebraska 2 mi or less.

The general surface of the land is not greatly diversified. Much nearly level land occurs, but rolling to hilly country predominates. Drainage is from an elevation of approximately 1,250 ft near the Nebraska-Dakota line to 850 ft in the southeast (Nebraska-Kansas boundary).

The soil has developed from transported material. Loess formed a mantle over glacial deposits in nearly all of the area, but in parts of it the covering of loess has been eroded away. Chief exception occurs in a relatively small part of northern Nebraska and southeastern South Dakota where outwash plains soil of gravel, sand, and finer materials are intermixed. There are extensive alluvial flood plains, 1 to 17 mi wide, along the larger rivers. In general, the soils are deep, fertile, fine-textured loams of high water-holding capacity and usually circumneutral in reaction. They all have great depth and are usually moist but not wet throughout.

Mean annual precipitation varies from about 34 in. in the southeast to only 23 in. in the northwest. There is usually a single period of heavy rainfall during the growing season. In the southeast this includes 5 spring and summer months but in the northwest only about 2.

Forest communities rapidly disappear along streams outward from the Missouri River, and the

typical condition is a mingling of upland trees with those of the flood plain. Farther from the great river, trees are mostly confined to the banks of larger streams and to broad shallow ravines tributary to them, or to the vicinity of springs. Some are found in the shelter of steep protecting bluffs. In the driest prairies trees occur naturally, if at all, only as small groups or as individuals in the most protected places.

The beginnings of woody vegetation at the headwaters of streams and its increase in kinds and number of species, as the stream provides a proper environment, will first be described. Then the results will be given of an extensive survey of the various types of vegetation which occupy the flood plains of the larger rivers.

Names of grasses are according to Hitchcock & Chase (1950) revised Manual of the Grasses of the United States. Other scientific names follow Gleason's (1952) New Britton & Brown Illustrated Flora.

ORIGIN AND DEVELOPMENT OF STREAMS AND THEIR WOODY VEGETATION

No land area is perfectly flat or perfectly smooth and much land is rolling or hilly. Although runoff water may at first form a thin sheet flowing evenly downward, it is concentrated by converging slopes into the shortest and steepest downward route. It is soon reinforced by water from runoff, seeps and springs from other hillsides and a definite stream is formed.

The headwaters of many streams have been investigated where they originated in unbroken prairie sod. At first the course is marked by an increase in abundance and stature of the more mesic grasses and forbs, especially big bluestem (*Andropogon gerardii*), when compared with those on adjoining slopes. Soon an intermittent stream, dry except after heavy showers, begins to cut into the sod to form a channel. As the channel deepens and widens along the first few miles of its course it presents a habitat where wind-blown seeds of willow and cottonwood may germinate and the seedlings develop. This may occur as soon as the soil is bared; then all along the stream, as isolated individuals or intermittent clumps, *Salix amygdaloidea*, *S. nigra* or *Populus sargentii* appear.

A few miles farther down the valley one may observe a slow, meandering stream, nearly dry in late summer but with banks 2-3 ft high, wending its way through wet meadow, or a spring-fed one which has ceased to be intermittent. The latter, joined by other streams, has cut its banks 10 ft wide or more and 6-8 ft deep. On both streams wind-protected, sloping banks were favorable sites for certain shrubs. Chief among these were coralberry (*Symporicarpus orbiculatus*), wolfberry (*S. occidentalis*), elder (*Samucus canadensis*) and indigobush (*Amorpha fruticosa*). Present in smaller numbers were smooth sumac (*Rhus glabra*), wild gooseberry (*Ribes missouriense*), frost grape (*Vitis vulpina*) and bitter-sweet (*Celastrus scandens*). Willows, 8-15 in. in diameter, and cottonwoods, a few 3-4 ft thick, were

much older and larger than those upstream. Green ash (*Fraxinus pennsylvanica*) and boxelder (*Acer negundo*) were sometimes represented by a few small trees. Farther downstream an increasingly large number of both trees and shrubs occurred as well as a beginning of their separation into different habitats. Fine large trees of red or slippery elm (*Ulmus rubra*) and white or American elm (*U. americana*) were most abundant on the banks. Flood plain species were boxelder, green ash, hackberry (*Celtis occidentalis*), honey locust (*Gleditsia triacanthos*), wild black cherry (*Prunus serotina*) and black walnut (*Juglans nigra*). Some of these, of course, grew near or among the elms as well as on the base of the slope. A scattered growth of young bur oak, usually with diameters of 5 in. or less, grew on protected north-facing slopes and sides of lateral ravines.

Aside from shrubs and vines found upstream, which occurred much more abundantly here, several other species had migrated upward from the Missouri River. These were roughleaf dogwood (*Cornus drummondii*), black raspberry (*Rubus occidentalis*), burning bush (*Euonymus atropurpureus*), green brier (*Smilax hispida*), poison ivy (*Rhus radicans*), virginia creeper (*Parthenocissus quinquefolia*), buckthorn (*Rhamnus lanceolatus*) and virgin's bower (*Clematis virginiana*). Most of these were scattered widely over the flood plain.

Continued study of the beginnings of vegetation along streams over this central prairie region, along branches of the Nodaway, Tarkio, Boyer, Elkhorn, and other rivers confirmed the general sequence described. Pioneer trees at the stream sources are those with light, wind-blown seeds such as cottonwood and willows. They usually appear soon after the sod is weakened by erosion. After a suitable habitat is available other species with wind-blown seeds occur, such as boxelder, elms and ash. The pioneer shrubs and vines—elder, coralberry, bittersweet, grape and others—have showy, edible fruits carried by birds. This early stage in woodland development is represented for considerable distances along nearly all small tributaries. It is especially pronounced in the western part of the area as well as northward, along the tributaries of such rivers as the Elkhorn and Big and Little Blue which extend far into the plains. When a stream develops a flood plain with wide protecting banks, large fruits such as walnut, bur oak, hickory, hazel, and others are carried up stream by various animals, especially timber squirrels. Thus, as soon as a suitable habitat is provided in wind-protected places along the stream, trees and shrubs may, in the absence of recurring fires, replace the prairie grasses. But on unsheltered and wind-swept banks of prairie streams, especially those far from large rivers, little or no woody vegetation may occur.

Far down most streams in the southeastern part of the area, flood plain forest is separated from bur oak and its border of shrubs by more mesic types of forest, especially red oak and linden.

CONTACTS OF WOODLAND WITH PRAIRIE

Prairie grasses may come in direct contact with trees, especially in the early development of woodland along streams. But usually grassland is replaced by shrubs which extend outward from the edge of the woodland. Of the several species concerned the most important are sumac, rough dogwood, coralberry and hazel (*Corylus americana*). Where shrubs extend into prairie it is by mass invasion. It occurs at a level above most of the prairie grasses and is due to shade cast by the peripheral plants leaning far outward toward the light.

Prairie vegetation is shaded out more or less completely under a closed canopy of sumac or other shrubs. For a time it may be completely replaced by kentucky bluegrass (*Poa pratensis*) which is nearly always present, at least in small amounts, among the other grasses; but ultimately bare soil may prevail.

Shrubs usually extended outward only a few feet or a few yards into prairie. Often their contact with upland prairie was with big bluestem which formed a thin border to the more xeric prairie grasses. On lower slopes a more or less distinct belt of switchgrass (*Panicum virgatum*) with canada wild-rye (*Elymus canadensis*) or sometimes cordgrass (*Spartina pectinata*) often intervened between bluestem prairie and shrubs.

A typical example of a low prairie-woodland contact follows. Transition from trees to prairie on a south exposure extended over only a few yards. Indeed, along a portion of the eroding creek both soil and trees had been washed away and prairie continued without change to the edge of the vertical bank. Elsewhere at the edge of the prairie the tall grasses were intermixed with an unusual percentage of coarse forbs such as oxeye (*Helianopsis helianthoides*), sawtooth sunflower (*Helianthus grosseserratus*), jerusalem artichoke (*Helianthus tuberosus*) and various species of goldenrod and aster. These first mingled with and then gave way to an intermittent border of roughleaf dogwood, coralberry and poison ivy. Elsewhere switchgrass and canada wild-rye extended to the shade and leaf litter under overhanging branches of the trees. A number of woody and herbaceous vines grew thickly at the forest edge and clambered over shrubs and far up the trees.

The west edge of this prairie, which was best protected from wind and afternoon sun, presented the widest, tallest and most varied fringe of shrubs. Here sumac formed thickets 8-15 ft high; thickets of wild plum (*Prunus americana*) were overrun by virginia creeper; frost grape and other vines were common and dense stands of dogwood, as tall as the sumac, were usual. Tangled vines of black raspberry were plentiful, and over much of the transitional zone poison ivy completely covered the soil with its thick foliage or climbed up the trees, the lower part of which were all but screened from sight by the mass of shrubs. A wetter part of this wide border was occupied by a thicket of sandbar willow (*Salix interior*).

Not infrequently saline areas occur locally or extend widely over the lower flood plains. Salt Creek

and some of its tributaries, for example, receive salty water through springs. Most prairie grasses are intolerant to salt. Hence, the wonderfully well developed bluestem prairies of the upper flood plain were usually separated from the woodland's edge by broad belts of salt grass (*Distichlis stricta*), western wheatgrass (*Agropyron smithii*) and other salt-tolerant grasses. Similar saline areas are common along the Platte, Elkhorn, and Missouri Rivers and hundreds of smaller streams.



FIG. 2. A typical forest of bur oak (*Quercus macrocarpa*) with undergrowth of various shrubs.

Contacts of upland prairie are usually but not always with bur oak woodland (Fig. 2). This oak often borders dry ravines as well as streams but it is rarely found in wet places. Where oaks occurred in dry ravines between steep hills, the wooded area was usually bounded by prairie right up to the edge of the banks; often shrubs spread outward only a little (Figs. 3, 4). Of the prairie grasses, the taller ones and especially big bluestem seemed to thrive best in the shade of the shrubs and especially under the shade of the branches of bur oak which spread outward near the soil. The half-shade often resulted in a



FIG. 3. Thicket of wild plum (*Prunus americana*) in blossom in spring along a ravine in unbroken prairie. Grasses are kept out by the shade.

border of blue grass on the prairie's edge under the shrubs and oaks. How far the shrubs extend outward is determined by the water supply and exposure to drying winds. Usually it is only a few yards.



FIG. 4. Mowed prairie with bur oak and other trees in a ravine along Oak Creek. Photo in August 1947.

As an eroded dry ravine gradually changes into one with running water, the flood plain trees become grouped nearest the water and the oaks on the upper slopes. Farther downstream where many rivulets joined to form a creek with wide sloping banks, the same general relationships occurred. These are maintained when a flood plain is developed—the oaks always on the high eroding banks; willows, cottonwood, elms and ash on the depositing ones.

Along the Platte where the bur oak forest clothed the sides of the bluffs facing the river, it soon gave way to prairie near their upper slopes or crests through a fringe of shrubs only a few yards wide. Here big bluestem tolerated the shade of open patches of these shrubs and often extended through the ecotone into the edge of the oak forest. In fact, large areas on the upper slopes and tops of the bluffs were a field of battle between grasses and shrubs; seedling oaks were rare.

On north-facing slopes, prairie often extended downward some distance on the ridges between the U-shaped, parallel ravines leading to the banks of the Platte River. The bur oaks farthest up the sides of the ravines were only 15-20 ft high and 9-14 in. in diameter. At a time when they were seedlings and saplings, they had been well protected from the drying southwest winds. The little bluestem prairie gave way slowly to the oaks in the ravines. A very open stand of wolfberry, dogwood and prickly ash grew among the grasses and, with kentucky bluegrass, under the oaks. Oaks increased in both number and size, and spreading outward replaced prairie on the intervening ridges. Woodland shrubs and vines such as gooseberry, black raspberry, grape and greenbrier, became common. But the narrow belt of bur oak was soon replaced by one of black oak, red oak and linden. This occurred first in the ravines but soon became general, and these trees extended downward to the

river. This sequence was repeated again and again on neighboring ridges, although the transition from prairie to bur oak was sometimes more abrupt and through a border of bluegrass resulting from the shade of the various shrubs.

Along the Missouri River the width of the chaparral on the bluffs beyond the bur oak forest in both Iowa and Nebraska varies from a few feet to 0.5 mi or more. The shrubs are fewer and the light values are generally higher near the outer margin of the zone than on its inner one near the oaks. In western Iowa, as elsewhere, bur oak may border the open prairie or give way to a zone of shrubs (Fig. 5).



FIG. 5. Forest-prairie border east of Audubon, Iowa. Hazel (*Corylus americana*) is the chief shrub, with small bur oaks in background. Photo, 1932.

Measurements in many areas of chaparral and prairie over periods of several growing seasons revealed that the shrub community had the higher water content, higher humidity, lower temperature, less wind, reduced evaporation and decreased light intensity. The oak can thrive usually only in protected valleys in the shelter of hillsides. On some bluffs along the Missouri River a strip of red oak and linden may occupy the lower slopes.

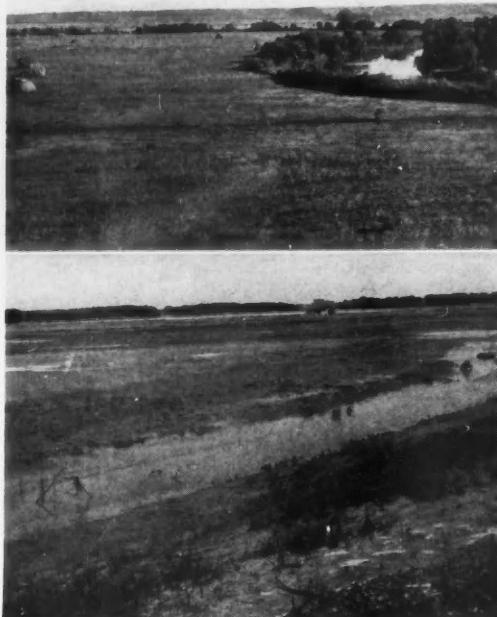
The tree communities of western Iowa are distributed along the streams and valleys and are best developed where they are well protected from drying southwest winds.

THE LARGER BOTTOM LANDS AND THEIR VEGETATION

Over the flood plains or bottom lands of the Missouri, Platte and lesser rivers, in addition to trees and shrubs which more or less border the rivers, plants of swamps, marshes, and three communities of grassland occur. Swamp plants live in the abundant shallow lakes and ponds or on the margins of deeper ones. Sedges and rushes occupy the marshes, where the soil is very wet in spring and early summer when it may be covered with several inches of water.

Coarse grasses, such as prairie cordgrass or switchgrass, occupy large areas of soil on higher ground than the marshes, but the largest grassland community is that of big bluestem which prevails mostly on second bottom lands where the soil is well drained.

The flood plain is a vast area of level lowland (Figs. 6, 7). Only when one observes it closely are slight changes in elevation noticeable. From the river's margin a distant view is obscured either by steep wooded bluffs on one side or on the other by trees, shrubs and vines of the flood plain forest. Since the apparently nearly level topography actually varies only a few feet below or above the general level, many habitats and various communities seem to the casual observer quite intermixed. Actually, as will be shown, there is a rather definite relationship between the kind of vegetation and the type of habitat which it occupies.



FIGS. 6, 7. (Lower) Republican River near Superior, Nebraska after the great flood of 1935. Much sand was deposited and later blown into low dunes. (Upper) Woodland along the James River in southeastern South Dakota and extensive hay meadows on the flood plain.

DEVELOPMENT OF FLOOD PLAINS

A river makes not only its own bed and channel but also the valley in which it lies is fashioned by the stream. The secular shifting of great river channels is recorded in the conformation of the plain. The flood plain of the Missouri River is 0.5-1.5 mi wide between South Dakota and Nebraska (Figs. 8, 9). In places southward it is 17 mi wide, but varies from 8-14 near the Kansas state line. The larger part of the flood plain in this area, perhaps 80%, is in Iowa.

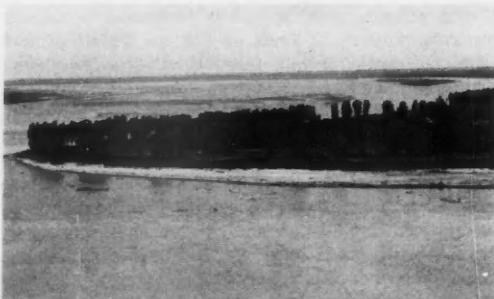


FIG. 8. Missouri River near Vermillion, South Dakota, showing young growth of cottonwood on a sandbar. The fringe of sandbar willow (*Salix interior*) has been eroded away.



FIG. 9. General view of bluffs facing northward along the Missouri opposite Yankton, South Dakota, showing trees along a ravine.

It is bordered on the east mostly by a broken line of bluffs, but in places only by hills. The channel often lies close to the steep bluffs which form the western boundary of the valley. The river is $\frac{1}{4}$ - $\frac{1}{2}$ mi wide where it begins to border Nebraska. Here the U-shaped valley lies about 150 ft below the summit of the immediately bordering bluffs. In southeastern Nebraska the bluffs bordering the wider, more mature valley are somewhat higher, some extending upward 250 ft. This river borders Nebraska for a distance of about 360 mi but because of its sinuous course the actual length is approximately 500 mi. The general elevation of the flood plain is about 1,250 ft where it first forms the South Dakota-Nebraska line and 850 ft at the Kansas-Nebraska border. The river's gradient is about 1 ft/mi along this portion of its course.

Streams in western Iowa flow more southward than westward (Fig. 1). The course of the Little Sioux River is more or less parallel with that of the Missouri and many of the southwest-flowing streams drain into it. The Boyer River crosses the flood plain north of Omaha; the Nishnabotna and Tarkio rivers run parallel with the Missouri River far into

Missouri before they empty their water into the main stream.

In Nebraska the general slope of the land is east and this determines the direction of flow of the rivers. The Platte, in the central part, is largest. This broad, shallow stream generally has low banks, but 20 mi or more from its mouth (Plattsmouth) the flood plain becomes narrower and the bordering hills and bluffs steeper. Its main northern tributary, the Elkhorn, flows southeast from its source in sandhill lakes and joins the Platte only a few miles from the Missouri. Salt Creek enters the Platte from the southwest but most of the southeast area is drained directly into the Missouri by the Weeping Water and Little and Big Nemaha Rivers. The Big and Little Blue Rivers reach the Missouri through northeastern Kansas by way of the Kansas River. Bluffs border many of the larger streams in part but often the valleys are bounded only by hills. Each river has its flood plain and many smaller streams meander through a plain 0.5 to 3 mi wide before entering the larger one of the Missouri.

The first bottom land of the flood plain is an expression of former channels of the river and materials which they constructed. Topography of the second bottom may result from the leveling processes of sedimentation by slack water from the river's flooding. Drainage out of the hills is mainly that of many small streams, often fed by numerous springs, that do not cross the flood plain but fill the ponds and lakes with sediments from the upland.

A stream or river when it rises and reaches the over-bank stage inundates the adjacent valley floor. When the overflow is spread out over the flat land its velocity is quickly and effectively checked. The heavier soil particles carried by the water are deposited along the immediate borders of the channel. These deposits take the form of low but distinct ridges, termed natural levees. They border the channel and remain after the flood has subsided. As flooding is repeated they are built higher until they become the most visible features of some valley floors. They may attain heights of 4-14 ft or even more but their heights are small compared with the depths of the channel. In the Missouri River this depth may be as much as 30 ft.

The part of any stream valley which is inundated during floods is a flood plain. In the course of floods the entire flood plain may be covered by a thin mantle of sediments which settles out from the lake-like shallow flood water that carried suspended finer silt and clay from the river.

A stream that rises in flood may overtop the natural levees in its down stream course. When the levees are breached at a weak point, the water flows rapidly down their outer slopes, which are much steeper than the gradient of the channel, and continues outward through new channels, leaving the old one with diminished discharge. Often the old channel is ultimately abandoned as a new one is formed. The new channel offers a lower level or a shorter course and it therefore gains on the old one

until it carries the greater volume of water. It is rapidly widened and deepened by the swift current. In the older one the current is slower and the sand and silt is dropped and the bed built up. Often a bar is built across the old channel which may then become a lake or slough. Sometimes several channels are developed forming a braided river. During such great floods the entire valley floor may be inundated except the trees growing along the main levees of the main channel. When a main stream breaks through a natural levee following ice jams, heavy rains or rapid melting of snow, the high-water stage has terrific force and may cause great damage.

Exceptionally high floods may inundate portions of the flood plain that the waters of usual spring floods do not reach. For example, a great flood occurred on the Missouri River in the spring of 1881. "The extensive bottom land was plastered with mud and sand: sites of farm houses were marked by piles of debris and by ruined chimneys; staunch barns were undermined, tilted, and rent with unequal settling, their doors and lower planking were torn away, and banks and bars of rotting grain marked the direction of the flood; the great corn cribs, hundreds of feet in length, were represented only by heaps of half-decayed corn . . . the fences were reduced here to scattered timber, there to tangled loops of barbed wire clinging to the stronger posts and clasping the carcasses of cows, horses, and swine; the railway track of a month before was scattered to right and left in hundred-yard links of rails and ties, the bent and twisted rails still grasped by a tie or two . . . in short, the fair land of a month before was replaced by a picture of utter desolation . . . one of the many reminders that man may not enroach upon the domain of a river with impunity" (McGee 1891).

Sinuous bends in a stream's channel, if they are fairly even and regular, are known as meanders. The Missouri and Platte are notable examples of meandering rivers. In meandering and shifting their courses, rivers may repeatedly abandon their channel and cut a new one in such manner as to leave a great loop in the river as an oxbow lake in the area of its flood plain. The oxbow is formed when the river cuts across the neck of a big bend or meander. As the lake is slowly filled with sediments, chiefly silt and clay, it becomes a pond and then a swamp or marsh. According to Longwell & Flint (1955) the river does not shorten its course especially by such cutoffs, because the lost mileage has been balanced by the enlargement of other meanders.

With each overflow, the natural levees on the river's banks become higher and the back-swamp more poorly drained, since this portion of the flood plain has not been elevated as rapidly as the stream bed. Where the natural levees come in contact with the uplands they prevent the escape of water collecting behind them and temporarily, pond or marsh conditions develop. At the edge of the valley, drainage out of the hills is mainly that of small streams that do not cross the flood plain.

As explained by Harper (1938) water in the

channels of tributaries flowing into the main river is also affected by the silting. Water in the channels of these streams must attain a considerable depth before it can flow into the main river, consequently the valleys have not only been filled with sediments but natural levees may also develop from the edge of the valley to the juncture of the tributaries with the larger stream. The combined effect of the cross levees prevents the escape of flood water collecting behind them. Materials suspended in runoff water flowing through these areas settles in the quiet water. Thus, deep layers of sediment may be formed.

Rivers, both large and small, as they flow through erodible land develop a flood plain. Such areas are commonly designated as bottom lands and more especially as first or low bottoms and second or high bottom lands. It has been estimated from several soil survey maps that along its course the Missouri River has 40 to 50% first bottom land. On first bottoms, especially within a mile or two of the stream, the river may occasionally change its course; but elsewhere such changes are to be reckoned in terms of hundreds or even thousands of years.

The Missouri River bottom is a nearly level plain of alluvial sediments. The topography is uniformly level, except in the relatively small areas where low ridges and shallow swales and slopes along the edges of old channels cause gentle undulations. Infrequently deposits of sand have been blown into low hills in local places. Usually the land has slopes of less than 2 to 3%. Meander scars are characteristic features of flood plains.

Fig. 10 was taken from a portion of the Craig, Mo.-Nebr. Quadrangle Sheet of 1920, supplemented by information from Corps of Engineers, Rulo to Yankton Survey of Missouri River, 1946-1947. It shows the braided and meandering Missouri flowing near the foot of bluffs which, as indicated by the contour lines, extend upward 150-200 ft above the flood plain. Also shown are cut-off lakes, the abundant larger marshes, sandbars (dotted areas) and islands, and a tributary river (Tarkio) and Little Tarkio Creek meandering across the flood plain. Here the valley varies in width from 5 to 14 mi. West of the main river and southwest of Bigelow the altitude is 861 ft and east of it, near the cut-off lake, 859 ft. It decreases only a few feet (to 858) near the Tarkio River but increases to 862 ft beyond the river. Thus, differences in elevation of only a few feet occur on this portion of the flood plain. The small flood plain of Squaw Creek (upper right), and the wide one of the meandering Nemaha River as it cuts through the row of bluffs (lower left) are shown.

FLOOD PLAIN SOILS

Low bottoms of the Missouri River present the following mixed alluvial land: Albaton, heavy soil (clays); Onawa, heavy soil of medium and moderately coarse clay over silt and sand; Haynie, soils of medium textures (loams and silts over sand); and Sarpy, a coarse sandy soil. Sandy soils often contain good supplies of most nutrients but are low in organic mat-



FIG. 10. A section of the Missouri Valley between Missouri and Nebraska just north of the Kansas-Nebraska boundary. The squares each represent 1 sq mi. Explanation in text.

ter and nitrogen content. These alluvial soils have been formed from recently deposited sediments and they lack distinct horizons. But they commonly do have layers which reflect the history of the stream. They usually occur near the river channel and are subject to occasional or frequent flooding, but they are moderately to well drained between overflows. They are occupied partly by trees, mostly willows and cottonwood, shrubs, sedges and rushes, and, in part, by various coarse, hydric grasses.

High or second bottoms of the Missouri and similar large streams present poorly drained Luton and Wabash clays and Lamoure silty clay loam. The Luton soil, a Wiesenboden or wet meadow soil, occurs mostly on the wider and flatter parts of the flood

plain, usually near the bluffs. On these wet meadow soils cordgrass, switchgrass, and wild-rye thrive. On Salix soil, a Brunizem (Prairie) soil of medium to moderately fine silt loams and clay loams that are mostly well drained, big bluestem is dominant. This soil occupies the slightly higher parts of the upper flood plain. Second bottom soils are flooded only rarely (Fig. 11).

Soils present in the small bottom lands of tributary streams are the somewhat poorly drained Leshara silty loam and Colo silty clay loam and the moderately well drained to well drained Kennebec and McPaul silt loam. These soils are mostly occupied by tall grasses chief of which is big bluestem. Trees often occur along the stream channel. The well

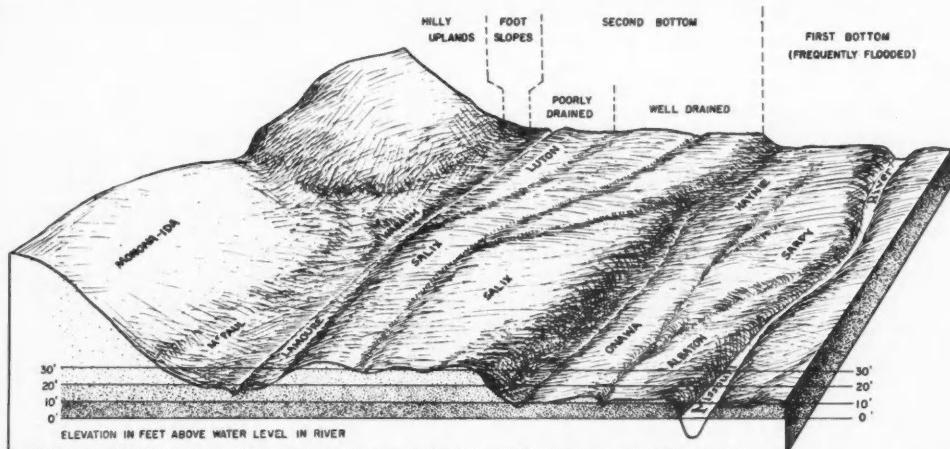


FIG. 11. Cross-section of the Missouri River flood plain showing position and relative elevation of the various soils in relation to the river. The Luton, Wabash and Lamoure soils are poorly drained because of runoff and perhaps seepage from hills and bluffs. Here lakes, ponds and marshes are frequent.

drained Judson silty loam at the foot of slopes furnishes an excellent habitat for big bluestem prairie.

Thus, a large number of soils, some water-logged, some poorly drained, others well drained and well aerated compose the bottom lands. Moreover, flooding, draining, and accompanying removal or deposition of soil are cyclic catastrophes. It seems clear to both the ecologist and the pedologist that it is not soil type per se that determines the kind and amount of native vegetation but rather aeration and constancy of water supply of these mostly productive soils that directly affects the vegetation. Generally these bottomland soils are neutral to slightly alkaline in reaction. When the land is placed under cultivation it is found that nearly every square mile presents several soil types.

A generalized diagram across a large flood plain is shown in Fig. 11. The width is several miles; the horizontal lines indicate the relative elevation or depression of the various portions of the flood plain. Separation of first from second bottom is often much less abrupt than is shown in the figure, but the difference in elevation is usually 10 or more ft. With a 10-ft rise in flood, the river water enters the channels of the first bottom. When the rise is 20 ft the first bottom is completely inundated and water enters the channels of the second bottom. A 30 ft rise in the river inundates all but the highest areas on the second bottom, and the entire valley may be covered with several feet of water in extremely high flood, but this happens very rarely. Fig. 11 is representative of conditions along the Missouri River in most places between Iowa and Nebraska. The writer is indebted to John Elder, Conservation and Survey Division, University of Nebraska, for figure 11 and to the Soil Conservation Service for much information on soils (*Cf. Simonson, Riecken & Smith 1952*).

FLOOD PLAIN FOREST

Flood plain forests along the larger rivers consisted very largely of cottonwood and willows. Along the Missouri they ranged from the water's edge over natural levees, to a distance of $\frac{1}{8}$ to $\frac{1}{2}$ mi from the river above Plattsmouth and to somewhat greater distances, in places, southward. In addition they bordered abandoned river channels, lakes and ponds. In the river they clothed great sandbars, and sometimes covered many acres of alluvial deposits on the inner or lower flood plain. The remaining area of the low, wet, first-bottom land was occupied by lakes, ponds, marshes, and in places by a luxuriant growth of coarse grasses often alternating or intermixing with various shrubs.

On the second bottom, forest occupied a very minor portion of the area. Here the supply of soil moisture resembles closely the type now found in prairie elsewhere. Soil development, with rare exceptions, clearly took place under a continuous cover of grass. It is possible that prairie fires had some retarding influence upon tree growth, but it seems more probable that the natural environment of moderate rainfall (23-33 in.), dry winds and long periods of summer drought, which characterize the prairie climate, were the determining factors.

Sandbar willow (*Salix interior*) is the first tree or shrub in this area to grow upon sandy or muddy banks of rivers, streams and lake shores. Its extremely abundant, fiber-like roots enable it to maintain a hold on the soil. This small tree, usually about 20 ft high, has a slender trunk 2-3 in. in diameter. In dense stands, which result from its spreading by long stoloniferous roots to form thickets, it is commonly dwarfed into a shrub only 5-6 ft high. Branches are slender, erect, and flexible. The elongated narrow leaves are light yellow-green. Saplings 3-6 yrs old often occur at the rate of 8-10/sq ft. Usually

there are few other plants in such dense stands. This willow is common in drying lakes and ponds, often intermixed with cattails and river bulrush, and also in marshes. Thickets of willows covering many acres are not infrequent. Sandbars in great rivers are often completely clothed with this species (Figs. 12, 13). Because of its stabilizing the soil, they may eventually become more or less heavily wooded. At Fremont and a few other places along the Platte and on several islands in the upper Missouri in this area, red cedar (*Juniperus virginiana*) also occurs on the lower flood plain and on islands in the river.



FIG. 12. A sandbar in the Missouri River mostly covered with sandbar, black, and peachleaf willow, with a few (taller) cottonwoods (*Populus sargentii*).



FIG. 13. Cottonwoods on Missouri River flood plain, showing their abundance along the small cut-off at the right.

Rivers are forever cutting away their banks in one place and depositing soil in another. Where the Missouri River forms a great bend, one may have an unobstructed view of the river-bank vegetation. The eroding side is often treeless, the woody vegetation having been undermined and swept away. Standing in the tall prairie grasses, one may look down from the eroding bank, where the water is deepest and moving most rapidly, and up and down the river for a mile or more. On the opposite or depositing shore one observes the continuous low zone of young sandbar willows, perhaps 50 yds wide. Beyond is a similar zone of older and taller willows, and still beyond are complete stands of tree willows (*Salix amygdaloides*, *S. nigra*). Still farther from the water's edge, a forest of stately cottonwoods towers upward to form the background of this magnificent scene.

The two species of tree willows are commonly 20-40 ft tall and 8-20 in. thick. They prefer the wet lower banks of streams and borders of lakes, ponds and marshes. They are intolerant of shade and usually form a border to the cottonwood forest which follows the river all along its course.

Cottonwood is the most typical tree on the banks of great rivers and often the only one on eroding shores where the fringe of willows on lower ground has been swept away. It is the only large tree on the banks of the Missouri and Elkhorn Rivers north of central Nebraska. Cottonwood grows rapidly and reaches a height of 70 ft or more, with trunks 3-6 ft in diameter. Where well lighted, as on the river margins or in open stands, branching begins low and scarcely higher than the shrubs. But in the forest the straight, erect or more or less leaning trees are free from branches to a height of 20-30 ft. Young trees have smooth, light yellow-green to nearly white bark, but on old ones it is ashy-gray, thick, and deeply furrowed into broad, rounded or narrow-edged ridges broken into scales (Fig. 14).



FIG. 14. Mature cottonwood trees with undergrowth of roughleaf dogwood (*Cornus drummondii*) on flood plain of Platte River.

Although flood plains usually bring to mind broad, level land, the site of this forest type is often very irregular. The river in flood has built up ridges and bars often 10 or more feet high running outward in all directions, with valleys, ravines, ditches, ponds and marshy places, all indiscriminately intermixed. Often the trees are scattered rather thinly, brush is only moderately abundant, and patches of lowland grasses may occur (Fig. 15). In other places trees are more closely spaced and thickets of young trees, shrubs and vines are so abundant that one can make his way over the irregular terrain only with great difficulty. An example of each type will be described; all intermediate conditions prevail.

As one proceeds from the water's edge, the thickets of low-growing willows give way to older ones, perhaps 20 ft high and less thickly spaced. Dense masses of various vines trail over the ground, climb up the trees and spread extensively through their branches. Frost grape is often the most abundant, although poison ivy and virginia creeper are



FIG. 15. View of the flood plain with cottonwood and willows and young elms on the Missouri near Omaha.

usually plentiful. The weight of the grape vines is so great that the willows are often bent down and their stems, although 2-3 in. thick, broken off at a height of 5-8 ft. Added to this tangled mass of vegetation are tree willows, many of which are leaning or have fallen and are overrun by false buckwheat (*Polygonum scandens*).

Next one may encounter a depression with a thicket of dead sandbar willows or areas of tree willows 30-35 ft high with trunks 5-11 in. in diameter. Beneath is a tangle of seedlings of cottonwood and willows. In more open places various shrubs and vines form a tangled mass of vegetation.

Wetter areas of a few square yards to several A in extent occur. Where the light permits its growth, nearly pure stands of reed canary grass (*Phalaris arundinacea*) may be found. By midsummer the leaves of this 5-8 ft high grass are dead and the plants often lodged, thus again making walking difficult. More often brush, consisting of dogwood, indigobush and prairie rose (*Rosa setigera*), and scattered willows, young cottonwoods and elms are intermixed. In still other places shrubs, cordgrass, switchgrass and dense patches of oxeye, american germander (*Teucrium canadense*), or tall sunflowers may occur. Thickets of plum, young cottonwood and elm are often so dense that there is no undergrowth.

Pools with cattails, arrowheads, and bordering sedge marshes may alternate with groups of tall, stately cottonwoods on the adjacent ridges, or with a dense undergrowth of patches of shrubs and vines.

Often the undergrowth of poison ivy is more or less continuous, at a height of about 2 ft, with vines climbing 20-30 ft on the trunks of trees. Lateral branches of the ivy sometimes reached outward 2-3 ft. Cottonwoods are differently spaced than are trees of upland forest. Near the river they nearly always occur on ridges in scattered groups of 2-10. The trees in a group often appear to be even-aged.

Elsewhere on the plain there are often wildernesses of sandbar willows, thriving, dying or dead, patches of tree willows with thickets of sapling red elm so thickly grouped that they are impenetrable. Similar patches consist of various shrubs—roughleaf dogwood, indigobush, wolfberry (*Symphoricarpos occidentalis*), sumac, prairie rose, prickly ash, elder (*Sambucus canadensis*) and others—all intertwined with vines of grape, virginia creeper and greenbrier. Interspersed are scattered trees, mostly young, of ash, mulberry (*Morus rubra*), boxelder, and an occasional honey locust. In this mixed vegetation grasses and forbs vary from complete absence to isolated bunches or small patches. The competition for light is so great that these plants elongate abnormally; species of smartweeds, american germander, western ironweed (*Vernonia fasciculata*), and tall goldenrods reach heights often twice those usually attained.

Added to the preceding are occasional masses of debris deposited during floods, fallen branches, uprooted trees, fallen logs, and occasionally dense stands of giant ragweed (*Ambrosia trifida*) 10-12 ft high, and other ruderals, often in abundance. This description may give a fair idea of the denser type of the flood plain forest of the Missouri and Platte Rivers.

Many cottonwood forests are far more open; one can walk through them with only minor deviations in his course. The large trees are widely spaced, often in small groups. Shrubs are abundant but occur singly or in small dense patches. Often enough sunshine occurs in openings to permit the growth of grasses. On many high, eroding banks where willows are few or none, great clumps of wild-rye, switchgrass and even big bluestem grow among the cottonwoods. But mostly cottonwoods alone occupy the banks; then the sandy soil is covered with a thin layer of fallen leaves and other debris. Elsewhere, a usually discontinuous understory of small trees, numerous shrubs and a layer of forbs prevail.

Scattered over the lower flood plain far from the river many cottonwoods of large size occurred. Some were 5-6 ft or more in diameter and 60 to 85 ft tall. Ring counts of stumps of similar trees revealed that they were 70-80 yrs old. On better drained alluvial soils farther from the river banks, many other forest trees are common. They are mostly red and white elm, ash (including white ash (*Fraxinus americana*)), boxelder and hackberry. They all prefer rich alluvial soils to river sand. Large trees are often infrequent; dead or dying saplings are common, resulting from poor soil aeration and deep shade. But on well drained, rich bottom lands, well developed specimens are abundant. Walnut (*Juglans nigra*) is not plenti-

ful except in the south, and there also sycamore (*Platanus occidentalis*) is a common flood plain tree.

Adjoining the flood plain, on the better protected slopes the red oak-linden community prevails along the Missouri River almost to Sioux City. It also extends 20-30 mi along the tributaries entering the lower portions of this river, linden ranging quite beyond the red oak. Where the stands are thick, fallen leaves cover the soil beneath the trees more or less completely.

It has been shown that flood plain forest is represented, even if poorly, along nearly all of the streams in the area. Willows represent the first stage; a little farther down the stream they become associated with the cottonwood and boxelder. On better developed flood plains, usually only a few miles from the head of the stream, red and white elm, and green and white ash become plentiful. The preceding species with the addition of hackberry and walnut and perhaps soft maple (*Acer saccharinum*), honey locust, kentucky coffeetree (*Gymnocladus dioica*), and sycamore (*Platanus occidentalis*) (southward) compose the typical flood plain forest of the broader more mature flood plains. Where the larger streams flow into great rivers much of the flood plain was forested. But northward and westward, under decreased rainfall, trees were generally confined to the moist, protecting stream banks.

The willow-cottonwood portion of the flood plain



FIG. 16. Well developed trees of american elm (*Ulmus americana*) on the flood plain of the Big Nemaha near Falls City, Nebraska. The largest tree is 3.5 ft in diameter and 95 ft high. Photo in 1928.

forest is especially typical of the Platte and Missouri rivers. It extends over low sandy banks, sandbars, abandoned channels and elsewhere. "A later development is shown by the growth of such species as *Acer negundo*, *Ulmus americana*, *U. fulva*, *Fraxinus pennsylvanica*, and *Juglans nigra*. These in turn may finally be replaced by *Tilia americana*, the elms often remaining as codominants" (Aikman 1929). The usual flood plain species occur on more stable and better drained soils of the broad flood plain between the bordering wooded hillsides or bluffs (Fig. 16). "The flood plain associes reaches its best development along the larger streams in the southeastern part of the area. . . . Since the shade is denser, fewer of the less tolerant species are found. The trees are much larger and in every way the flood plain forest better developed. Secondary species are *Fraxinus americana*, *Padus virginiana*, *Gymnocladus dioica*, *Aesculus glabra*, *Celtis occidentalis*, and *Platanus occidentalis*. The shrub stage is not as prominent as in the previous stage because of reduced light" (Aikman 1929).

According to Aikman, in the absence of devastating floods over long periods "the flood-plain may finally be built up to a place where the soil becomes sufficiently well drained and aerated to permit the growth of climax dominants. . . . The advance of red oak and especially linden into such areas has been repeatedly observed and sufficiently studied to show the trend of development toward climax forests."

Common shrubs of the flood plain forest, which also extend far beyond the forest margin and intermingle with coarse grasses, are as follows; those near the end of the list are usually of least abundance.

<i>Cornus drummondii</i>	<i>Rhamnus lanceolatus</i>
Roughleaf dogwood	Buckthorn
<i>Amorpha fruticosa</i>	<i>Rubus occidentalis</i>
Indigobush	Black raspberry
<i>Symporicarpos occidentalis</i>	<i>Rosa setigera</i>
Wolfberry	Prairie rose
<i>Symporicarpos orbiculatus</i>	<i>Zanthoxylum americanum</i>
Corallberry	Prickly ash
<i>Rhus glabra</i>	<i>Cornus stolonifera</i>
Smooth sumac	Red osier
<i>Prunus americana</i>	<i>Euonymus atropurpureus</i>
Wild plum	Burningbush
<i>Sambucus canadensis</i>	<i>Rubus allegheniensis</i>
American elder	Common blackberry
<i>Ribes missouriensis</i>	
Wild gooseberry	

Roughleaf dogwood is one of the most abundant. Dense stands may skirt the forest edge and thickets 8-10 ft high with little undergrowth may extend outward over many square rods. Indigo bush, of similar height, is most abundant around ponds, in marshes and on the wet banks of ditches. Elder also thrives best in wet places. Smooth sumac mostly borders the sunlit openings or occurs on the forest edge. In the southern part of the area buttonbush (*Cephaelanthus occidentalis*) grows in low wet soil.

The following woody vines were usually common and often abundant: frost grape (*Vitis vulpina*),

bittersweet (*Celastrus scandens*), greenbrier (*Smilax hispida*), poison ivy (*Rhus radicans*), virginia creeper (*Parthenocissus quinquefolia*) and virgin's bower (*Clematis virginiana*).

EXTENT OF FLOOD PLAIN FORESTS

The writer, in 1954, summarized forest and prairie on flood plains as follows: "On the wide alluvial bottomlands of the larger rivers, of both eastern and western prairies, the forests were often limited to relatively narrow strips along the channel and the abandoned oxbows, alternating with strips of prairie." This is in accord with the observations of early explorers, pioneer settlers, and early land surveys, and is confirmed by studies of scientists in the early part of the present century.

Bradbury (1809) reports: "I availed myself of this opportunity to visit the bluffs [across the Missouri River near Omaha] four or five miles distance from us, on the north-east side. On approaching them I found an extensive lake running along their base, across which I waded, the water in no part reaching higher than my breast . . . Its surface was much covered with aquatic plants. On gaining the summit of the bluffs, I was amply repaid by the grandeur of the scene that suddenly opened to my view . . . and looking into the valley of the Missouri from an elevation of about two hundred and fifty feet, the view was magnificent: the bluffs can be seen for more than thirty miles, stretching to the north-eastward in a right line, their summits varied by an infinity of undulations . . . The flat valley of the Missouri, about six or seven miles in breadth, is partly prairie but interspersed with clumps of the finest trees through the intervals of which one could see the majestic but muddy Missouri."

Schaffner has been intimately acquainted with the prairies of Kansas since 1871, at a time when the original conditions prevailed. He states in 1926: "The first bottom of river flood plain, where a normal soil had developed, was largely occupied by a typical *Andropogon furcatus* prairie, due to the action of prairie fire which was continually destroying the forest belts developed in the river bends and confining them to narrow strips . . . The second bottom was ordinarily too dry to permit of tree growth. Only the low flood plain, deep ravines, and steep protected slopes are potential forest habitats in the absence of fire."

Sampson (1921) lists numerous extensive grassland areas along the Mississippi and Illinois rivers in Illinois, and Turner (1934) states that the flood plain forest is confined to a belt or zone a few hundred yards to a half mile in width paralleling the river channel or surrounding ponds and lakes. The landward side of this forest type merges into a grassland association.

It is believed that along our section of the Missouri River the flood plain forest, shrubs and coarse grasses occupied most of the first bottom but that the second bottom was nearly all covered with prairie. Exceptions of course occurred around ponds and

lakes and on poorly drained land. It has previously been pointed out that the well drained Salix soil has developed under a cover of prairie grasses, and the less well drained Luton soil under coarser, wet meadow grasses (Fig. 11).

The Missouri and Platte rivers have very wide valleys and although the bordering bluffs and hills furnish protection against the prairie climate, this protection does not extend throughout their width (Fig. 17). In fact, some of the best developed flood plain forests, with a great variety of trees, occur in the protection afforded by wooded bluffs and steep hillsides where tributary streams with relatively narrow flood plains join the main rivers. It is interesting to note that trees on the upper edge of the protecting slopes are of lower stature than those on the lower slope. Indeed, the canopy of trees bordering streams is often nearly level.



FIG. 17. Flood plain of the Platte near Fremont, Nebraska showing trees along the river in background and the wide expanse of grassland. Photo July 15, 1929.

The kinds of flood plain communities, in addition to forest, and their interrelations are of importance to an understanding of grasslands.

SWAMPS

The reed-swamp stage of the hydrosere is well represented in lakes and ponds both large and small which occurred by the thousands and were especially widely scattered over the flood plains of the principal streams. A lake may be defined as an inland body of standing water occupying a basin; a pond, as a lake of slight depth. Swamps are places where the normal summer water level is continuously above the soil surface.

The dominant species of swamps are relatively few; all are large, coarse perennials. They are great bulrushes (*Scirpus validus*, *S. acutus*), river bulrush (*S. fluviatilis*), broad-leaved cattail (*Typha latifolia*), reed (*Phragmites communis*), bur reed (*Sparganium eurycarpum*), arrowhead (*Sagittaria latifolia*) and water plantain (*Alisma*). "A peculiar feature of marshes [swamps] of this type is the readiness with which the individual facies may become isolated, or localized, notwithstanding their coherency in marshes [swamps] of considerable extent (Pound & Clements

1900)." While these dominants are often intermixed, much more frequently one species may occupy vast areas almost to the exclusion of others. Plants which root on the bottoms of swamps occupy definite places, which are related to the depth of the water, silting, and characters of the substrate. They form definite and often pure communities. The great bulrushes usually grow in the deepest water, sometimes in excess of 6 ft, cattails at intermediate depths, and reeds in the shallowest. All have large, much branched rhizomes, and where establishment of seedlings is unsuccessful invasion is still possible.

Swamp plants have such a wide distribution and are so conspicuous that they are known by most students of botany. Hence, only brief descriptions and emphasis on certain features will be given.

Scirpus validus and *S. acutus* vary greatly in stature. The narrow, terete culms on the edge of drying lakes may be only 3 ft tall and less than $\frac{1}{4}$ in. in width; in the most favorable habitats they are 7-11 ft high and $\frac{3}{4}$ in. in basal diameter. They are perennial from tough, slender or stout rhizomes. Often 8-12 culms occur per sq dm. But usually the culms are more openly spaced even when in dense clumps. Vast areas of river banks, swamp land and shallow water were occupied by great bulrushes previous to the drainage of the flood plain. In many lakes they bordered the shores in water 1-5 ft deep continuously for several miles.

Cattail (*Typha latifolia*) is one of the most common and abundant species of swamps. Where shallow water permanently covers the surface of the soil it almost always occurs. The plants grow thickly in dense, mostly pure stands, yet the individuals do not seem crowded. This results from the nearly erect position of the leaves and the spacing of the clumps along the large thick rhizomes. If the habitat is congenial they spread rapidly to occupy the space; if it becomes dry, the plants are greatly stunted and finally die. Height varies greatly, often it is 5-7 ft above the water level, with some leaves extending well beyond the spikes. But robust plants more than 9 ft tall with basal dimensions of 2x4 in. and about 14-in.-long leaves up to $\frac{3}{4}$ in. in width are not uncommon. Cattails often border ponds in a wide zone, and near the shores of lakes they often extend in shallow water as a continuous stand for miles. Fassett (1940) states that propagation by rhizomes is so efficient that an entire community may develop from a very few plants. Enormous amounts of debris result from the death of parts above ground in winter.

Aside from other swamp dominants, cattail stands usually have few other species, except the free-floating duckweeds (*Lemnaceae*) which are present from early spring to late fall. The narrow-leaved cattail (*Typha angustifolia*), of common occurrence here mostly since 1900, is far less abundant.

The reed (*Phragmites communis*) occurs in pure stands in swamps and on banks of streams, where many hydric species, common elsewhere, fail to thrive. This coarse perennial grass has a complex system of rhizomes, which may occupy the soil 8-10 in.

in depth; erect culms are 8-12 ft tall. In addition, very long, horizontal stolons may occur. Always conspicuous because of its rapid growth and great stature, it is especially so during flowering, when the long hairs of the spikelets develop in such manner that the whole flowering portion is a silky mass.

Some experimental work has been done at Lincoln, Nebraska, to test the establishment and competition in three typical swamp communities where *Scirpus validus*, *Typha latifolia* and *Phragmites communis* grew. Separate communities of bulrush and cattails grew along a sluggish stream and reeds about a pond. Reciprocal transplants were made during a period of three years (1923-25). From the results it was concluded "Although both *Scirpus* and *Typha* are occasionally found scattered through the *Phragmites* community in nature, they are to be regarded as relicts. The water content of such areas is too low for them, especially in late summer of dry years, and the dense and continuous layer of rhizomes of *Phragmites* practically prevents their invasion . . . The paramount factor in their elimination is shade, the great stature and broad spreading leaves of the reed-grass reducing the light intensity to a decisive degree (Clements, Weaver & Hanson 1929).

River bulrush (*Scirpus fluviatilis*) inhabits river banks and shallow water and is very widely scattered over the flood plains (Fig. 18). The abundant, thick rhizomes of this perennial promote rapid spreading. The coarse, stiff stems are triangular in cross-section and reach heights of 4-6 ft or more. The long leaves



FIG. 18. River bulrush (*Scirpus fluviatilis*).

spread widely. This bulrush occupies great areas of swamps and is sometimes intermixed with species of marsh plants.

Scirpus atrovirens is an abundant bulrush scattered widely in wet areas over the first bottom land. It is a coarse perennial with thick rhizomes and grows in dense tufts to a height of 3-5 ft. The 8-10 leaves, about 0.5 in. broad, are mostly on the lower portion of the culms. It usually occurs in places somewhat wetter than those occupied by cordgrass. The dark-green foliage and abundant brown spikelets, the scales becoming black with age, makes this plant conspicuous both in dense patches and when intermixed with other species.

Scirpus maritimus is a perennial rush of very common occurrence, usually in shallow fresh water and in alkaline swamps. The rhizomes that produce the 3-angled culms also develop tubers. The plants in figure 19 grew in a pure stand covering a 0.5 A; the 4 in. of water darkened the base of the culms which reached heights of about 2.5 ft. The spikes are not yet fully developed.



FIG. 19. *Scirpus maritimus* (left) with spikes in early stage of development. *Iris versicolor* (right) about 2.5 ft tall on June 12.

Scirpus americanus is also a perennial rush which occurs in shallow water or on very wet soil. From the long, tough rhizomes, triangular, stiff culms extend upward to a height of 3-5 ft. The sparse leaves are 12 in. or less in length. The single to several grouped spikelets appear to arise from the side of the culm near its end, since the single bract is a continuation of the culm. This rush is often abundant.

Bur reed (*Sparganium eurycarpum*) has stout, erect leafy stems usually only 2-4 ft tall (Fig. 20). The leaves are shallowly and broadly triangular in cross-section. The plants grow in shallow water, usually in extensive, dense stands and they are of very common occurrence.



FIG. 20. Sweet flag (*Acorus calamus*) (left) 3-4 ft tall with linear spadix covered with yellowish-brown flowers. Bur reed (*Sparganium eurycarpum*) (right) about 3 ft tall in fruit.

Arrowhead (*Sagittaria latifolia*) often grows in the shallow water or mud bordering the cattail zone in belts a few feet to many yards in width and an A or more in area. A dozen leaves 8 in. wide and 12-18 in. long may be produced per plant. They form dense stands with a nearly complete foliage cover. In the soil there are dense mats of roots, and rhizomes with tubers 1-2 in. thick (Figs. 21, 22).

Sweet flag (*Acorus calamus*) not infrequently grows in local, almost pure stands bordering areas of bur reed or arrowhead. Common associated species are spike rush, cursed crowfoot (*Ranunculus sceleratus*), and water foxtail (*Alopecurus geniculatus*). It is also found in the wetter portions of marshes.

Other plants of common occurrence and often of great abundance are water plantain (*Alisma*) and, especially northward, indian rice (*Zizania aquatica*). The last is of special interest since it germinates under water, passes through a submerged and floating stage, and then emerges to produce a plant often 7-8 ft tall. A single plant may spread over several square feet.



FIG. 21. Arrowhead (*Sagittaria latifolia*) growing in shallow water.

The lakes and ponds were also inhabited by water lilies, anchored by roots and rhizomes in the mud 3-8 ft below the water surface (Fig. 23). The leaves sometimes covered the water with floating mats of green over hundreds of acres. Elsewhere pondweed (*Potamogeton*) grew in wide expanse. Equally characteristic were the tiny plants of duckweeds, *Lemna* and others, often so abundant as to form great sheets of green.

MARSHES

Marsh is a term denoting a type of vegetation rooted in an ordinary nonorganic soil that is waterlogged. The water level in summer is close to the soil surface but normally not much above the ground level. In spring or following heavy rains the soil may be flooded. When the soil in swamps is built up to or rises above the water level, marsh plants begin to colonize the areas once occupied by bulrushes and cattails. Phragmites, because of its extensive rhizomes which range in depth from 1 to 10 in., may persist for a time among the marsh plants. This stage in the hydrosere is sometimes designated as the sedge-meadow stage (Weaver & Clements 1938). Small marshes along stream banks and on the edges of ponds have already been mentioned, but they occur most extensively, covering hundreds of square miles, on poorly drained or undrained flood plains of

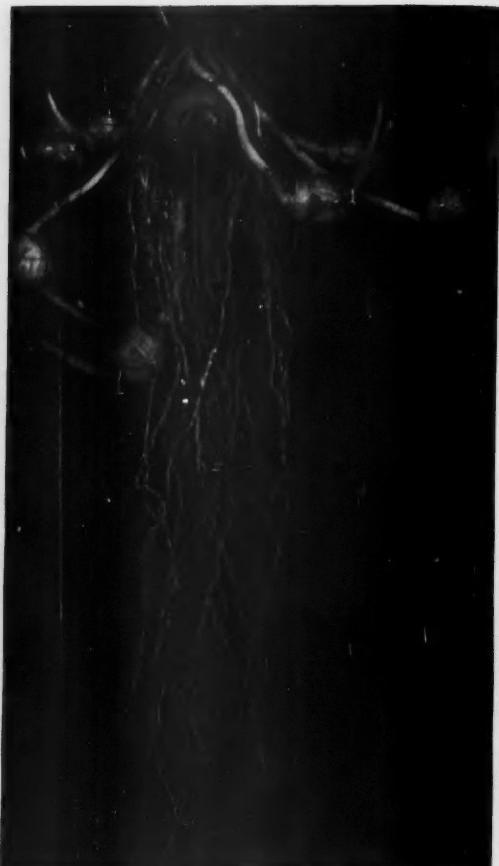


FIG. 22. Underground parts of arrowhead—roots, rhizomes and tubers.

large rivers. Species of marsh plants, especially various sedges and certain hydric grasses, may occur intermixed with swamp borders of arrowhead, and often the marsh extends quite to the edge of the zone of cattails. On the drier side, marshes give way to cordgrass or other coarse grasses.

Some marshes are inhabited almost entirely by tall species of *Carex*, *Juncus* and *Eleocharis*; others consist largely of species of hydric grasses such as rice cutgrass (*Leersia oryzoides*) and reed canary grass; but usually they consist of a mixture of species from the preceding genera intermixed with grasses and forbs. Marshes, usually of smaller extent in wet ravines and depressions in wet land, are often entirely populated by forbs, mostly of the smartweed genus (*Polygonum*).

In general appearance marshes do not differ greatly from lowland prairie; the densely grouped mostly perennial and sod-forming species of sedges have grass-like foliage which begins growth very early and attains a height of 2-3 or more feet early in June. The plants frequently grow in open bunches



FIG. 23. Zones of white water lily (*Nymphaea tuberosa*), bur reed, and sandbar willow.

but rhizomes are common and with the abundant fibrous roots they often form a dense sod. A very large number of species compose the marsh vegetation but only a few of the most abundant ones will be noted.

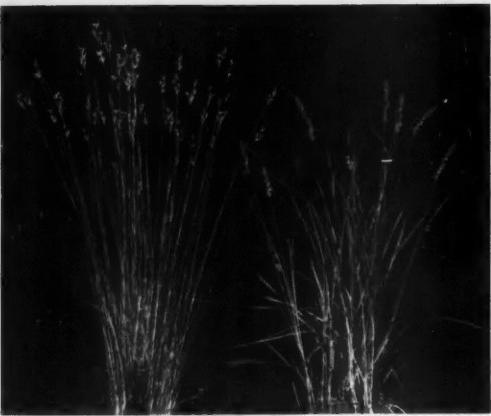


FIG. 24. Fox sedge (*Carex vulpinoidea*) (right) nearly 3 ft high and in fruit on July 5. A rush (*Juncus tenuis*) (left).

Carex vulpinoidea, fox sedge, grows in dense tufts and alone or with other species forms a compact sod (Fig. 24). The stiff, upright stems have an abundance of long, grass-like leaves. Stands are dense and often nearly pure except for swamp milkweed, fringed loosestrife, and other hydric forbs. The extensive rhizomes produce 5-20 stems per square decimeter and the foliage entirely conceals the soil. The shade is dense and frequently the debris is 5-7 in. deep. As a dominant it may form small patches or cover extensive areas. It often forms distinct zones around ponds or other bodies of water. Early growth results in foot-high plants in April and twice this height in June. When in fruit, in late June or July, plants are often 2.5-3 ft tall. This species is of very common occurrence and often alternates with cord-

grass or is intermixed with it as an understory. In hundreds of places that are too wet for prairie grasses, it forms alternes often of such great extent they may compose half of the entire vegetation. Usually it is associated with other tall sedges such as *Carex lasiocarpa*.



FIG. 25. *Carex lasiocarpa* on May 20, showing both staminate (upper) and pistillate flowers. Height is about 3 ft.

Carex lasiocarpa is a rhizomatous plant with flat, very long attenuated leaves which are often 5 mm wide (Fig. 25). A height of 2 to more than 3 ft is attained late in May. It often forms nearly pure stands over considerable areas, but it is also mixed with other sedges and rushes. It occurs abundantly on wet banks or in shallow water bordering bur reed swamps, and is commonly associated with western water hemlock and stiff marsh bedstraw. Like the preceding species it frequently composes a considerable part of marsh-land hay.

Carex sprengei is a tall sedge often associated with *C. vulpinoidea* but it also grows in nearly pure stands. It is abundant along streams and frequently composes much of the marsh vegetation, especially in the northern section of the area. Rhizomes are numerous and the culms are usually less than 3 ft in height.

Carex lupulina forms dense tufts by means of short, stout rhizomes. Figure 26 shows a small portion of an old bunch with a basal area of more than a square foot and a circular top 3 ft in width. The plant is usually 1.5-3 ft tall. The larger leaf blades are 1 to more than 2 ft long and average nearly 0.5 in. in width. The hundreds of cylindric al, pistil-



FIG. 26. *Carex lupulina* with broad leaves and an abundance of pistillate spikes. Height is 3 ft.

late spikes are very conspicuous. It is a characteristic species of shallow swamps and marshes. This species like *C. lurida* and certain others, extends into shallow water on small hummocks of earth and also grows thickly on the muddy edges of ponds.

Carex stricta was once abundant over the area where it formed extensive patches characterized by the culms forming large stools or patches in swales and marshes. Costello (1936), who has made a thorough study of tussock meadows in southeastern Wisconsin, states: "Tussock meadows are dominated by a single species, *Carex stricta*, which produces tussocks that consist of a tuft of leaves and culms at the summit of a pedestal composed of roots, rhizomes, soil, and vegetable debris. New tussocks are initiated by means of rhizomes which grow horizontally from the bases of old tussocks. Individual tussocks may attain a height of 2-4 ft and a diameter of 30 in. They may persist in an area for many years." Marshes were found along the Elkhorn River where the tussocks were elevated above the soil 12-18 in. Since the clumps were separated by distances of 1-3 ft and the interspaces were obscured by the overhanging dense foliage of the 3-ft tall plants, walking was difficult although the soil was not wet. Only a few of the preceding sedges and other marsh plants occurred here. In other places this sedge was found in water about 12 in. deep.

Carex festucacea grows in dense clumps; the long, slender, erect culms hold the flowers quite above the foliage (Fig. 27). It occurred abundantly from very



FIG. 27. *Carex festucacea* about 2.5 ft tall and in fruit.

wet to rather dry soil. It ranges from soils with relict cordgrass, where it may compose a large percentage of the vegetation, to typical marshy land where it intermixes with other species or grows in pure stands. *Carex hystericina*, *C. lacustris*, *C. crinitella* and *C. interior* are other species of wide distribution and considerable importance.

Among the rushes, *Juncus tenuis* is perhaps the species of greatest abundance. The numerous stems, usually about twice the height of the foliage, are loosely to closely spaced in tufts. They extend outward and upward to approximately twice the height of the narrow leaves (Fig. 24). This perennial is distributed widely from marshes with *Carex vulpinoidea* to wet meadows. On lowland subject to overflow or very high water content in spring it frequently forms extensive patches and constitutes 1/4-1/2 of the vegetation.

Torrey's rush (*Juncus torreyi*) often occurs in abundance in marshes and wet soil. The conspicuous inflorescence of many heads on one stout, rigid, erect stem is characteristic, as are also the tuber-like thickenings on the underground parts of this rather tall (2-3.5 ft) perennial.

The rushes as a group are far exceeded by sedges both in number of species and in importance in the vegetation of marshes. Several species of *Cyperus*, especially *C. erythrorhizos*, are found commonly in marshes and other wet places, especially in sandy soil.

Eleocharis palustris is the most abundant of the spike rushes. It often occurs in nearly pure stands. Perennial by creeping rootstocks, the annual crop of



FIG. 28. Spike rush (*Eleocharis palustris*) (left) 3 ft high with achenes fallen from the shattered spikelets. *Cyperus erythrorhizos* (right).

terete stems forms much debris (Fig. 28). It varies in height from 8 in. in drier swales to 1.5-3 ft in continuously wet soil or in shallow standing water. This species is most conspicuous in spring and early summer over many acres of low, poorly drained land. The spike rushes, including especially the much smaller *E. acicularis*, form great alternes with or frequently an understory to other marsh plants and even grow under thin stands of cordgrass. Like most hydrophytes, this species renews growth early. Normally plants are several inches high early in April and a month later the spikes are developing. This is followed by blossoming in June and July. Where *Eleocharis palustris* is dominant few other plants are associated with it. *E. obtusa*, a much smaller annual plant without rootstocks, is also common on marshy land.

Smartweed sometimes characterizes marshes in wet ravines and depressions in flood plains and wet meadows. Among the chief species are *Polygonum natans*, *P. lapathifolium*, and *P. coccineum*. The last includes aquatic forms with floating or submerged stems as well as terrestrial forms with erect stems often 3 ft high. Other important species are *P. punctatum*, *P. hydropiper*, *P. hydropiperoides* and *P. pennsylvanicum*. Often singly but sometimes intermixed, they form dense vegetation with few other plants, from muddy stream banks to extensive shallow depressions that are dry in late summer. Height varies greatly, from 1-6 ft. Some species are annuals, others are perennials with creeping stems and well

developed rhizomes. Flowers are small but extremely abundant. They vary with the species from greenish to white and pink to rose-red or scarlet.

Since most marsh grasses as well as many forbs also extend widely over the lower flood plain, they will be described along with the coarse grasses of wet lands.

Extensive marshes occurred along the Elkhorn River near Norfolk, Nebraska. One, 80 A in area, was studied in August, 1952, about 3 mi west of the city. Here the flood plain was about a mile wide; the marsh on the first bottom was approximately 10 ft lower than the second bottom where big bluestem prairie was being cut for hay. Everywhere the soil was wet, since the water table was close to the surface. Some places were muddy and in others there was 1-2 in. of standing water. The soil was mostly a sandy loam. Although the topography appeared to be level, there were variations of a few feet. Flat land and low ridges alternated with depressions and small, shallow ditches.

The vegetation consisted entirely of plants characteristic of marshes; bluestem grasses were not found and cordgrass was nearly absent, at least in its characteristic stands. Various carices composed the bulk of the abundant, lush vegetation, which grew to a height of 2.5 to 3.5 ft. It completely hid the soil and had relatively few forbs except in alternes of species of smartweeds. *Carex lasiocarpa*, *C. sprengelii*, and *C. vulpinoidea* were usually the most abundant species. They grew so thickly, in pure stands or intermixed, that walking was difficult. The matured plants were of a bluish-green color; fruits were often so abundant as to add a brownish tinge; the lower portions of the plants were a dull brown, and unlike bluestem prairie there were no flower stalks extending high above the foliage.

Composition of the vegetation varied greatly. In places the tall, stiff, triangular and almost leafless stems of *Scirpus americanus* were scattered thinly to thickly. Elsewhere it formed dense, extensive and almost pure stands, which indicated somewhat wetter soil. These were marked by the dark-green color and abundant brown spikelets. Various carices occurred in variable abundance. Among these were *C. cristatella*, *C. lurida*, *C. lacustris* and, in a few places, *C. stricta*. Spike rushes grew in distinct patches and often in continuous stands. In slightly wetter places, the vegetation consisted of small to large patches of considerably dwarfed *Scirpus atrovirens*. This bulrush was more or less mixed with various sedges but its brown umbels made it conspicuous. *Juncus torreyi* was also common and with *J. tenuis* grew in patches.

Portions of this marsh were clothed with stands of smartweeds often 3 ft high and so dense that most other vegetation was excluded. Chief species were *Polygonum coccineum*, *P. natans* and *P. lapathifolium*. They also intermixed in part with other marsh dominants. Reed canary grass claimed a place in this area, growing in pure stands. Tufts of both northern reedgrass and bluejoint were found and

redtop was scattered thinly in places. Species of horsetail (*Equisetum*) should be mentioned since they were abundantly represented.

Typical coarse marsh forbs were *Eupatorium perfoliatum*, *Asclepias incarnata*, *Cicuta maculata*, *Apo-cynum cannabinum* and *Aster paealtus*. In the understory, where vegetation was less dense, *Galium tinctorium*, *Steironema ciliata*, *Stachys palustris*, *Lycopus americanus* and *Mentha arvensis* occurred. Although this list could be greatly enlarged, forbs in general were not abundant. The great mass of hydric vegetation began growth early and soon shaded the soil so completely that many forbs did not thrive.

This great growth of vegetation is utilized by the farmer either as pasture or a poor type of hay, since the soil is usually dry enough to permit hay making in late summer. But where the land can be drained it is far more valuable for farm crops. The present area, like thousands of other marshes, was later drained and is now producing hybrid corn.

COARSE GRASSES OF WET LANDS

Coarse grasses which occupy great areas of flood plains and are intermediate in habitat requirements between plants of marshes and big bluestem prairie, on their drier side, will now be considered. They are predominately prairie cordgrass on the wetter part and switchgrass and canada wild-rye on land less well drained than that occupied by big bluestem prairie. The vigor and great size of these coarse grasses, the extent of their holdings and density of stand can scarcely be overemphasized. Usually cordgrass is rather clearly separated from switchgrass and wild-rye.

Prairie cordgrass (*Spartina pectinata*), but sloughgrass to the pioneers, is the most abundant grass of the lower flood plain and wet lands wherever they may occur. It almost alone occupied hundreds of square miles along the great rivers and their tributaries throughout the true prairie. It grows on the wet banks of sluggish streams and about ponds but rarely in moist soils except in dry cycles or as relicts in soil which has been drained. On its hydric side this grass is usually bordered by tall rushes, sedges and marsh grasses. A good stand of cordgrass indicates that without drainage the soil is too wet for the production of corn. The soil, like that of the marshes, may be covered with water during a period in spring.

Except for the reed and perhaps eastern gama grass (*Tripsacum dactyloides*), this is the tallest and coarsest grass in the area (Fig. 29). It has a tough, coarse and much-branched system of rhizomes which occupy the surface 8 in. of soil and with the thick, cord-like roots of great depth firmly bind it in place. Stout stems vary from 5-15 mm in diameter. They range from 5-10 ft in height and occur at the rate of 1-3 per sq dm if large, but average about 6 where plants are smaller. The stem has 6-10 leaves with sebrous margins, which are sometimes nearly $\frac{3}{4}$ in. in width and 2.5-5 ft long. The conspicuous panicles are 1-2 ft long and 4-8 in. wide. Maximum flower-



FIG. 29. A typical dense stand of prairie cordgrass (*Spartina pectinata*) on a flood plain. The plants are 6 ft tall; photo July 13.

ing occurs in mid-August. The plants usually form a complete cover and in dense stands almost no other plants are found. Here the foliage to a height of about 2 ft soon becomes yellow and dry. This warm-season perennial renews growth early and extends upward more rapidly than other prairie grasses. Early in June it is usually in the fifth- or sixth-leaf stage and 2-3 ft high (Fig. 30). Yields are large, 3-5 T/A and in some experimental plots they were even greater. When mowed for hay 2-3 cuttings are made annually. Smoothness of the leaves makes the hay difficult to handle; it easily slips off the hayrack or from the haystack.

The ability of this grass to stabilize the soil and resist water erosion is indeed great. Where steep banks of streams, that run bank full during heavy rains, are clothed with prairie cordgrass, the rushing water, once the grass has been lodged, has only slight effect in removing the soil. This has been fully confirmed experimentally; it was shown that soil held by the rhizomes and roots and covered with the wet slippery leaves of this grass reduced soil erosion almost to nil. Moreover it is much less injured by moderate soil deposit than are most grasses; the hard, sharp-pointed shoots push their way upward through a foot of sand or silt. These characteristics, together with its rapid growth from seed, make clear the way in which this grass succeeds in maintaining itself on the ever-shifting soils of the lower flood plain.



FIG. 30. Relative height attained by prairie cordgrass in background and switchgrass (*Panicum virgatum*) in foreground on the Missouri flood plain on June 24.



FIG. 31. Eastern gama grass (*Tripsacum dactyloides*).

To keep one's bearings while walking in a great field of cordgrass is extremely difficult because distant vision is quite obscured by the 6-7 ft foliage. When dry, the mass of plant materials, far greater than in bluestem grassland, is an enormous fire risk and any trees or shrubs that had possibly succeeded in competition with the grass for light would surely be destroyed by fire.

Eastern gama grass is a tall coarse plant that is abundant and often the sole dominant over extensive areas of wet lands in the southeastern part of this study area. It also forms alternates with cordgrass and is found intermixed with wet land sedges on the one hand and well watered big bluestem on the other. Thus, it has a wide range of habitats from seepage places on hillsides, along ravines, and over the flood plains. It renews growth in March from extremely large and compact rhizomes. Early in May it is 7-13 in. tall and the massive foliage is 3 to nearly 4 ft high by mid-July. Flower stalks appear late in June and increase the total height to 5-7 ft. A single flower stalk may give rise to 3-5 branches, which with the main stem are terminated with conspicuous inflorescences 8-10 in. long (Figs. 31, 32).

Both small and very large circular bunches are produced. These range from 1-2 to 3-7 ft or more in diameter. They produce 15-25 flattened and somewhat woody stems/sq dm. Smaller stems are 2x8 mm in diameter but larger ones may be 5x10 in width. The 7-10 leaves per culm are coarse and frequently 0.5 to 1.3 in. wide and 2-3 ft in length. Under the widely spread and dense foliage few other plants



FIG. 32. Rhizomes of eastern gama grass.

survive. When unmowed and unburned a mulch 1 ft deep soon accumulates. Old circular clumps are frequently hollow within and here slight invasion by bluegrass may occur. A single cutting sometimes yields 3 T/A, and often three cuttings are made during the growing season.

Thousands of acres of first bottom land along the Missouri and its tributaries are covered with marshes, cordgrass, and with wet meadows of switchgrass, virginia wild-rye and other coarse grasses. All are subject to occasional flooding and soil deposit. Often the vegetation is considerably mixed and numerous forbs and grasses occur more or less throughout, except where they are kept out by deep shade.

Phalaris arundinacea (reed canary grass) is a

coarse perennial very common in wet places too poorly aerated for most other grasses. The greater height and glaucous color of the foliage makes this grass conspicuous in contrast to the darker green of sedges among which it frequently grows. It often occurs in patches but also spreads widely and the total amount is very great. Like most species of low ground, where competition for light is severe, it rewards growth early from a vast system of coarse, deep, tangled rhizomes. New shoots are a foot high in April, and in July the foliage is 2.5-3.5 ft tall and the shade is dense, since the abundant, flat leaf blades are almost 0.5 in. wide. Mature plants range from 2.5-8 ft in height (Fig. 33). The conspicuous panicles are 3-18 in. long and spread widely during flowering. They may turn brown by midsummer; lower leaves to 1.5 ft in height also may die, and with the preceding year's foliage form so much debris that walking in this grass becomes very difficult.



FIG. 33. Bunch of reed canary grass (*Phalaris arundinacea*) about 6 ft tall.

Leersia oryzoides (rice cutgrass) grows in wet soil or shallow water, often at the edge of zones of arrowhead. It covers extensive areas in marshes, on river banks, and around willow thickets on the flood plain. Its slender, weak culms, often decumbent at the base, reach heights of 2-4 ft. Plants are connected by slender rhizomes. Both leaf sheaths and blades are light green and so retrorsely pubescent that they cut ones hands and tear at ones clothes, in such a manner that progress over the thick grass is slow.

L. virginica (whitegrass) is of similar habit but it is much less abundant.

Glyceria striata (foul managrass) is found in wet places, especially where big bluestem gives way to wetter grassland. Usually it composes but a small part of the vegetation, but in local areas this tussock-forming plant often makes up more than half of the vegetation.

Elymus virginicus (virginia wild-rye) occurs frequently and often abundantly in and near marshes and along streams. Sometimes it forms an understory to cordgrass. Stems of this perennial occur in dense tufts. They are erect, rigid and leafy and usually 3-3.5 ft high. The thick spikes are 2-6 in. long and mostly erect. This important species is also found in open woods and is widely scattered over flood plains. *Muhlenbergia racemosa* is likewise widely distributed in wet areas and especially near brush or woodland.

Agrostis alba (reddtop) is a rhizomatous grass 2-4 ft tall. It often occurs in pure stands, forming alternates with various sedges, spike rush or cordgrass, but it is also intermixed with them as isolated clumps. The rather short flat-bladed leaves do not cast a dense shade, hence an understory of kentucky bluegrass may occur even in places densely populated by reddtop.

Poa pratensis, an introduced rhizomatous species, occurs in small amounts more or less regularly in all of the wet-land communities but is often absent or in small amounts in dense shade.

Other grasses of marshes include *Beckmannia syzigachne* (american sloughgrass), *Calamagrostis inexpansa* (northern reedgrass), *C. canadensis* (blue-joint) especially northward, *Cinna arundinacea* (stout wood reed), and *Alopecurus aequalis* (shortawn foxtail).

Certain forbs are constantly associated with the more open stands of cordgrass and may be intermixed with other grasses of wet land. *Fragaria virginiana*, *Oxalis stricta* and *Viola papilionaceae* are of low stature. *Galium tinctorium*, *Steironema ciliata*, *Anemone canadensis*, and *Teucrium canadense* form an understory 1.5-3 ft high. An intermediate layer is composed of *Asclepias sullivantii*, *A. incarnata*, *Coreopsis frondosa*, *Verbena hastata*, *Apocynum cannabinum*, and species of *Polygonum* and *Rumex*. Very tall plants are *Helianthus grosseserratus*, *H. giganteus*, *Heliotropis scabra*, *Cicuta maculata*, *Silphium integrifolium*, *Aster paeonifolius* and *Solidago altissima*. *Equisetum arvense* is common throughout the bottomlands. The evergreen, solitary or clustered stems of *E. hiemale* are also common to abundant. They are sometimes about 0.5 in. thick and extend upward 3-5 ft.

TRANSITION TO BIG BLUESTEM PRAIRIE

Panicum virgatum and *Elymus canadensis* compose a community of coarse grasses which thrive under soil-moisture conditions intermediate between those of cordgrass and big bluestem. Where the land slopes very gradually, broad areas are occupied by this type; but where the changes are more abrupt

cordgrass may be separated from the big bluestem community only by a narrow belt of switchgrass and canada wild-rye. Moreover, extensive mixtures occur on both margins. Switchgrass is more abundant southward, wild-rye increases in abundance northward.



FIG. 34. Typical stand of switchgrass 3.5 ft tall on June 24. The old flower stalks of the previous season are 5.5 ft high.

Switchgrass is a tall, coarse, sod-forming species. It seeds abundantly and established plants renew growth in April. By early June, the foliage is often 18 in. tall. The dense foliage completes its growth by mid-July (Fig. 34). The leaves are 8-14 mm wide and 1.5-2 ft in length. They are usually 6-8 per stem. Foliage height of mature plants is mostly 3-5 ft but the panicles increase the total height to 5-8 ft. They begin to appear in late July, and at maturity are 1-2 ft long and 16-24 in. wide. More than 300 panicles may occur in an area of 1 sq m. The coarse stems are 6-15 mm thick. This species easily qualifies as one of the coarser flood plain grasses, which occupied thousands of acres of flood plains.

Canada wild-rye attains a height of 3-4 ft by the middle of June. Then the spikes begin to appear. With the elongating stem they add another foot in height. Stems are rather woody and stout. The leaves are broad but only 8-16 in. long. It may form pure stands locally but is more often inter-

mingled with switchgrass. It grows intermixed with cordgrass in wetter places and with Indian grass and big bluestem in drier ones. It is of sufficient abundance to rank as one of the more important flood plain grasses.

Examples of the transition follow. On an 80-A prairie of the Missouri flood plain near Bigelow, Missouri, the higher portion was dominated mostly by switchgrass in dense, pure stands or intermixed with canada wild-rye. Relict cordgrass gave way slowly to large bunches of switchgrass and then to the switchgrass sod, except that ribbon-like extensions of cordgrass continued in the switchgrass along a few swales. Virginia wild-rye also became much less abundant. Enough drainage occurred along the high part of the very gentle slope to permit the growth and dominance of big bluestem and Indian grass (*Sorghastrum nutans*). These at first occurred as isolated bunches or more or less circular patches but soon they formed the bulk of the vegetation. Switchgrass and canada wild-rye then became the subdominates.

With the transition from wet, poorly aerated soil to conditions of good moisture and good aeration, there was also a gradual change in other species. Hydrophytic species, as water smartweed and swamp milkweed dropped out. Shrubs, such as indigobush, roughleaved dogwood and elder became rare; but stiff marsh bedstraw, fringed loosestrife and meadow violet remained plentiful in the understory. Species commonly found associated with big bluestem became abundant for the first time.

Along the Platte River many examples were found on the nearly level, wet, sandy soil where big bluestem became intermixed with switchgrass which graded into a nearly pure stand, and then gave way in swales to cordgrass, which, in turn, was replaced on wetter land by extensive marshes. Similar changes on flood plain from big bluestem to switchgrass and then abruptly to enormous bunches of eastern gama grass occurred in Kansas and Missouri. These are examples of scores of other grasslands examined many years ago along the flood plains of various large rivers.

Thus, it seems clear that the transition from cordgrass to big bluestem prairie is nearly always through an area or belt of switchgrass and canada wild-rye. This is also often the same for eastern gama grass.

In the description of lowland vegetation the types or communities have been emphasized. Amount and depth of water and chance distribution of propagules both play a large part in plant distribution. Not only do the same communities occur repeatedly but they are often greatly disturbed and intricately intermixed in patches and zones. The patterns are as diversified as the distribution of meander scars, lake shores and other sites for flood plain forest, or shallow water for swamps, saturated soils for marshes, and areas both large and small of half-dry and dry land.

On the best land of the second bottoms the soil is drained, even if poorly in some places, and the

water table is usually several feet below the soil surface. Of the tall grasses composing the lowland prairie, big bluestem is nearly always the chief dominant. Indian grass is of secondary importance as are also switchgrass and canada wild-rye.

Where much sand is deposited on the flood plain the wind often blows it, when dry, into ridges and low hills. Sometimes bluestem prairie, broken and cultivated for several years, has been buried under several feet of sand. Such areas are usually populated by needlegrass (*Stipa spartea*) and various species of grasses and forbs characteristic of the great sand hills of central Nebraska.

Sand hills are developed to some extent on the flood plain along the Republican River. Here may occur sand reed (*Calamovilfa longifolia*), sand lovegrass (*Eragrostis trichodes*), sand dropseed (*Sporobolus cryptandrus*), sand paspalum (*Paspalum stramineum*), lance-leaved psoralea (*Psoralea lanceolata*) and cactus (*Opuntia macrorhiza*). All are species common in the Great Plains sand hills. Along the Platte, Elkhorn, and certain other rivers there are many sandy and sometimes gravelly deposits. Most of the alluvium has come from the soils of the uplands in a particular watershed over a long period of time.

Where sandy ridges occur along the Nemaha, the big bluestem on the surrounding heavy black clay loam is almost completely replaced by needlegrass. Areas of many acres on the flood plain of the Missouri are characterized by low sand dunes and sandy soil. Sandy and sandy loam soils along the Platte River are very extensive. Here one finds many of the species characteristic of sand. The type of natural vegetation clearly reveals the extent of the sand. Thousands of acres of sandy lands are used only for grazing. Other less sandy soils, often intermixed with clay loams, furnish vast areas of highly productive land for native hay, as along the valley of the Elkhorn River (Fig. 35).



FIG. 35. Typical flood plain along the Elkhorn River. The great expanse of grassland furnishes an abundance of hay.

Although the flood plain of the Missouri, like the uplands, was early laid out along section lines (sq mi), roads were relatively few and many section lines had none. This resulted in part from open water

and wet land but mostly because of the smaller number of farms. In early days the farmsteads were mostly located on the foot-slopes at the margins of the flood plain. But this varied greatly with the width of the plain.

The flood deposits of the Missouri River, including the natural levees, were built up over a long period, but the process has been interfered with by the engineering works (mainly dikes built of earth and concrete) designed to prevent the river from generally inundating its flood plain. The natural levees have been artificially heightened by earth dikes to hold the floods, while at selected points spillways have been built to allow the water of the highest floods to escape harmlessly into natural channels that roughly parallel the river.

After the turn of the century locally organized and controlled drainage districts were formed. The lakes and marshes at the margin of the flood plain were filled with soil from the uplands by directing the water from the hills into them. Here the transported soil settled out and ultimately filled them. The water evaporated from these settling basins and ordinarily did not travel farther over the flood plain. Other low places were built up in a similar manner. In addition thousands of drainage ditches, many 6-10 ft deep, were constructed, often on every section line, to drain the soil and carry the water through proper channels to the river.

Today 75-90% of the land is under cultivation or is pastured (Simonson, Riecken & Smith 1952). Very little of the land is used for production of hay. Furthermore, drainage projects along many of the tributary streams have made the entire flood plain, to the very edge of the old channel, suitable for farming and thus destroyed the natural vegetation. The writer has witnessed much of this change. Modern machinery has contributed greatly to the rate of this destruction of the natural vegetation. Levees or dikes could be built far more extensively and other water control structures and deep drainage ditches made and maintained everywhere with the use of tractor-drawn machinery and draglines. The forests could be removed in a short period of time. To clear the land of towering cottonwoods, the pioneer ringed the bark and thus killed the trees, which were burned standing the next year or two. After the first quarter of the century great bulldozers uprooted the trees which were then dragged into windrows where they were consumed by fire after the wood had dried. In wet and often sandy soil the roots of the cottonwood do not penetrate deeply but spread widely, thus forming a flat-bottomed base.

The descriptions thus far have endeavored to picture the vegetation in its original condition, as a scientific record of the past. Today, even the big bluestem prairie, which covered most of the second bottom, has all but disappeared.

COMMUNITY LIFE IN BIG BLUESTEM PRAIRIE

Typical native grassland even in the more westerly parts of True Prairie has almost been replaced by

closely grazed pastures and plowed fields. This is especially true of big bluestem prairie which occupied the most fertile soil of the lowlands. In the early decades of the present century this prairie was mowed each autumn for its large yield of excellent hay. With an increase in the population, better drainage of lowland soils, and the replacement of horses by the tractor, most of the sod was broken and the land used for the production of cultivated crops. The change has been so widespread that it is now difficult to locate even small representative areas. These prairies were studied from 1918, through and after the great drought of 1934-41, until the land was finally broken.

Big bluestem (*Andropogon gerardii*) was the most abundant species which occupied the broad valley of the Missouri River and the valleys and ravines of its tributaries. It also grew thickly on lower, well watered slopes. Almost pure stands occurred over extensive areas and this grass alone usually composed 80 to 90% or more of the vegetation. It does not thrive in soil that is frequently saturated, but here gives way to switchgrass and prairie cordgrass.

The total basal cover of the vegetation averaged only 12%; much soil surface remained unoccupied. Yet the foliage was so dense and light so greatly reduced that invasion by other plants was difficult. Growth is very rapid, a dense layer of foliage 3 ft high is produced by midsummer. Then stout flower stalks, each with 9-10 leaves, extend upward 7-10 ft (Fig. 36). In this dense vegetation a few other

grasses, chiefly Indian grass, Canada wild-rye, and switchgrass occur in small amounts. In addition very numerous perennial forbs ranging from 6 in. to 15 ft in height, grow, flower and ripen seed in inter-spaces not occupied by the grass.

In early spring the prairie appears dull-brown or gray. The September mowing leaves a stubble 2-4 in. high. Except where mowing is early, there is little aftermath and the soil is usually clothed with only a half inch of litter. Against this drab background the new green blades are very noticeable, and especially societies of forbs in bloom are conspicuous. None attained a height greater than 12 in. until late in May when they elongated somewhat in response to the shade of the rapidly developing grass. Altogether they occupied only a small part of the soil surface.

Species of the prevernal aspect are all relatively shallow-rooted perennials. All are of low stature and blossom and ripen their seeds rapidly in an area which is well lighted for only a few weeks in spring. Flowering of some may continue into May. Plants of some species then disappear above ground; others linger on in the dim light of the understory.

In the early days of May the prairie changes in appearance from that of winter. Big bluestem is 1-3 in. high and its new green soon obscures the bases of the old stems. Although Canada wild-rye and switchgrass were 6-8 in. tall, they were not abundant, and there were not enough forbs, except locally, to relieve entirely the drab aspect of winter. All vegetation was now growing rapidly; big bluestem during May grew at the rate of 0.5 in. per day, and by the end of the month its shoots had about 6 leaves and a general foliage height of 16-18 in.

The numerous forbs of the vernal aspect developed so rapidly and attained such heights that they completed flowering before they were overtapped by big bluestem or other tall grasses. Moreover, the summer-blooming forbs grew so rapidly that nearly all equaled or exceeded the grasses in height. Forbs blooming in autumn stood out conspicuously above the grasses.

The last week in May witnessed the completion of blossoming of most vernal forbs. The landscape was rapidly redecorated with species and societies of summer.

At the beginning of the summer aspect the tall grasses had attained a height of at least 16 in. Forbs had extended upward even more rapidly and thus maintained a place in the light. The summer bloomers were gradually overshadowed by the foliage of the grass which by mid-July reached a general level of 2.5-3 ft. But willow aster and tall goldenrod, both autumnal bloomers, extended upward from 2 ft on June 1 to 4 ft in mid-July, and saw-tooth sunflower from 3 to nearly 9 ft.

Late in July the appearance of the prairie gradually changes. The bluestem foliage has now almost completed its development, and forms a deep cover 2.5-3 ft thick. Thus, the average rate of growth was more than 0.5 in. per day. The great mass of vegetation had a profound effect on modifying the amount



FIG. 36. Big bluestem (*Andropogon gerardii*) about 8 ft tall early in September. A typical scene along many upper flood plains.

of water of soil and air, wind, and light. Despite the large amounts of water daily transpired, the soil remained well supplied except during the most severe years of drought. Even in the surface foot 5-15% was nearly always available for growth, and at greater depths to 6 ft, 15-20%. These conditions were ascertained by weekly soil sampling in various prairies over a period of several growing seasons. The still deeper soil was also well moist.

Average day humidity during drier growing seasons (but not in drought) was about 50-65% and during moist ones 60-95%. These data are from self recording instruments placed at a height of about 6 in. in undisturbed big bluestem prairies. Relative humidity was almost always higher near the soil surface than in or above the foliage of the grass. But even above the foliage at noonday, humidity was often 50%. Midsummer determinations near noonday at a height of 1.5 ft, for example, gave readings 8 to 15% higher than at 3 ft. Near the soil surface the humidity was further increased 3-8%. Wind near the soil surface, after the vegetation had established complete cover, was almost nil. Late in summer only 2-5% as much air movement as that above the vegetation occurred at 2-3 ft in height.

Light was the chief limiting factor to plant development. The forbs of early spring always remained near the surface of the soil where for a time they received full sunlight. At the beginning of the vernal aspect the grass was only 2-3 in. high. Thus, during the long days of May the new crop of forbs was at first well lighted. Moreover, these plants grew somewhat taller than the prevernal ones; hence their competition for light was not severe. But with the rapid growth of the bluestem, light at 12 in. height was reduced to 15-20% of full sunshine, and near the soil surface to only 3-5%. As the season progressed, light in the understory became progressively less.

It is during the autumnal aspect, in August and September, that blossoming of big bluestem reaches its maximum. At this time the flower stalks stand 4-5 ft above the foliage level of early July. When examined in September, a lateral view of the prairie clearly exhibits its layered structure. This is beautifully shown during the process of mowing. Plants, or their dried remains, of most of the prevernal species may be seen as well as those of the vernal aspect. Plants of this lower layer scarcely extend to heights greater than 8-16 in., and the layer is by no means continuous.

A middle layer, which is much more prominent, occurs at a height of 1.5 to about 3 ft. The great mass of vegetation in the upper layer of forbs consists of rosinweeds, sunflowers, asters, goldenrods and other coarse plants of the autumnal aspect. These vary in height from 4-15 ft.

These layers of forbs by themselves, however, do not constitute the vegetation. By full adjustment in time and place, nature produces these varied species in a framework of grasses so dense that one penetrates it on foot with difficulty, and so tall that one

might easily become lost in the maturing vegetation of a single growing season.

Thus, the vegetation changes from a simple open structure of early spring to a more complex one with a middle layer as it grows higher with the progress of the season. Finally, with the development of an upper layer of forbs, and the lengthening of the flower stalks of grasses, mostly in late summer and autumn, a very complex structure results. Throughout the three major aspects the controlling vegetation is big bluestem. The habitat usually supplied excess of factors for growth—water, nutrients, light and heat—after the demands of the dominants had been met. The intensive utilization of these factors is possible because of the plan of life in the prairie is so diverse. As the season advances there is a constant shifting and readjusting as the component species of higher layers continue to develop and increase their stature.

Early in September of a normal season the green color of big bluestem, Indian grass, and switchgrass is slowly replaced by the red and bronze and golden tints of autumn. As the season progresses these colors gradually deepen until the landscape presents a color scheme of exquisite beauty and delicacy of painting. But before this time is reached, ordinarily comes the mower. This tremendously varied and intermixed crop is harvested and only the stubble, like that of the preceding spring, remains. But this is essential to maintain prairie as it has been described; the rebuilding will begin once more come spring. If the mass of dead plants is not removed by haymaking or fire, or kept from accumulating by grazing animals, the grassland as described will deteriorate after several years and become quite unlike that known to the original white owners, which condition has been faithfully described (Weaver & Rowland 1952).

SUMMARY

A long-time study has been made of the origin and development of streams in prairie and the woodland vegetation which often borders them. Contacts of the woodland with prairie have been described. The area examined extended about 350 mi along the axis of the Missouri River and from the Mississippi-Missouri divide in Iowa westward about 200 mi to the edge of the Great Plains. Special consideration was given to the development of the bluff-rimmed flood plain of the Missouri and other large rivers.

Most of the 23-34 in. of rainfall is absorbed by the deep, granular prairie soil, but following heavy rains or rapidly melting snow on frozen soil, water from converging slopes flows downward into ravines. At first the course of the headwater is marked only by a more luxuriant growth of grasses and forbs, but as the intermittent stream cuts into sod to form a channel, wind-blown seeds of various species of willows (*Salix*) and cottonwood (*Populus*) produce the first woody vegetation. Joined by other branches, some of which are spring-fed, a channel several feet wide and deep is formed in the course of a few miles and the stream is no longer intermittent. Ash (*Fraxi-*

nus), boxelder (*Acer*) and elm (*Ulmus*), all from wind-blown seeds, become scattered along the banks. Several species of xeric shrubs and vines with fleshy, bird-carried fruits appear. Farther down-stream a flood plain is developed on which hawthberry (*Celtis*), walnut (*Juglans*) and other trees and an ever increasing number of shrubs and woody vines thrive after migrating upstream from the deciduous forest along the bluffs of the Missouri between Nebraska and Kansas and Missouri. Where sheltering hills or deep canyons occur, a woodland of bur oak may occupy the sheltered slopes but contacts prairie on its upper margin. Unless well protected the upper flood plain may remain as prairie.

Where more mesic forests of red oak, hickory and linden occur in the southeast they extend from the outer edge of the flood plain upward along the bluffs. The bur oak occupies the uppermost slopes or hilltops and contact with grassland is usually, but not always, through hazel (*Corylus*), sumac (*Rhus*), coralberry (*Symporicarpos*) and other shrubs in a belt of a few feet to 0.5 mi in width.

The larger bottom lands, their development, soils, and vegetation, have been described. The flood plain of the Missouri River is 0.5-1.5 mi wide between South Dakota and Nebraska but 8-15 mi wide southward. A river makes not only its own bed and channel but also fashions the valley through which it flows. The secular shifting of great river channels is recorded in the conformation of the plain. The Missouri is more than $\frac{1}{4}$ mi wide where it begins to bound Nebraska and the bluffs bordering the valley are about 140 ft high. It borders Nebraska for a distance of 350 mi but because of its sinuous course the actual length is approximately 500 mi. The river's gradient along this portion of its course is about 1 ft/mi; southward the wooded bordering bluffs may extend upward 250 ft above the flood plain.

The first bottom land of the flood plain is an expression of former channels of the river and materials which they constructed. Soils of the mixed alluvial land formed from recently deposited sediments lack distinct horizons. They vary from heavy clays, heavy clays over silt and sand, loams and silt over sand, to coarse sand. They usually occur near the river channel and are subject to occasional or frequent flooding. These soils, sometimes covering 40% of the plain, are occupied partly by trees, mostly willows and cottonwood, shrubs, sedges and rushes, and, in part, by various hydric grasses.

Topography of the second bottom land, which is often 10 or more feet higher, may result from the leveling processes of sedimentation by slack water from the river's flooding. Drainage out of the hills is mainly that of many small streams, often fed by numerous springs, that do not cross the flood plain but fill the ponds and lakes with sediments from the upland. Second bottoms of the Missouri and other large streams present poorly drained clays and silty clay loams. The poorly drained wet meadow soil occurs mostly on the wider and flatter parts of the flood plain, usually near the bluffs. On the wet

meadow soils prairie cordgrass (*Spartina*), switchgrass (*Panicum*) and wild-rye (*Elymus*) thrive. On Brunizem (prairie) soils of silt loams and clay loams, occupying the higher parts of the upper flood plain and mostly well drained, vast prairies of big bluestem are found. Second bottom soils are rarely flooded. Topography of the flood plain, names and locations of the various soil types, and their relation to flooding are clearly shown by means of drawings.

Flood plain forest consists mostly of various willows and cottonwood, ranging from the water's edge over natural levees to a distance of $\frac{1}{8}$ to $\frac{1}{2}$ mi, northward, and to somewhat greater distances, with increase in number of species, south of Plattsmouth. They also border abandoned river channels, lakes and ponds, but are mostly confined to first bottom land. They are best developed where protected from drying winds by sheltering bluffs. Sandbar willow is the first to become established on river banks and it thickly populates sandbars. Black and peachleaf willows, 20-40 ft tall, are abundant. Cottonwoods, with trunks 3-6 ft thick, tower upward 60-80 ft. Other flood plain trees, such as those along smaller flood plains, also occur, sometimes abundantly. These forests have been described as well as the undergrowth of shrubs and woody vines.

Vegetation of the numerous swamps and extensive marshes has been described. Bulrushes (*Scirpus*), cattails (*Typha*), reed (*Phragmites*) and bur reed (*Sparganium*) grew in water 1-8 ft deep in dense stands often extending as far as the eye could see. Marsh vegetation is rooted in waterlogged soil where the water level in summer is close to the soil surface. Chief species were the grasslike sedges 2.5-3 ft high, many of which are pictured and described. Spike rushes (*Eleocharis*), smartweeds (*Polygonum*), water hemlock (*Cicuta*) and many other forbs such as iris and various mints inhabited the marshes. The total area occupied by marshes was very large.

Great areas of the flood plains, intermediate in drainage between the marshes and bluestem prairie, supported continuous grassland of prairie cordgrass. It grew in dense stands from thick rhizomes. The stout stems were clothed with leaves about a half in. in width and 2.5-5 ft long. Foliage height ranged from 5-7 ft and the dense shade often excluded most other plants. Other wet-land grasses were rice cut-grass (*Leersia*), virginia wild-rye (*Elymus*), reed canary grass (*Phalaris*) and redtop (*Agrostis*). Shrubs were often intermixed and also a large group of tall coarse herbs.

Transition from this wet-land vegetation is through narrow to very wide zones dominated by switchgrass, a tall, coarse sod-forming species, and canada wild-rye, also a coarse grass but of somewhat lesser stature.

The rapid growth and almost complete dominance of big bluestem on the best drained soils and its possession of the major portion of second bottoms have been discussed. Community life in this prairie, the changing structure of the vegetation with the progress of the season, and the wonderful productivity of the prairie soils have all been considered.

This study, begun in 1916, has endeavored to picture the native vegetation in its original condition, as a scientific record of the past. After the turn of the century drainage districts were formed. Lakes and marshes at the margins of the flood plain were filled with soil from the uplands by diverting the water from the hills into them, where the transported soil settled out. Later powerful modern machinery was used in clearing away trees and digging deep drainage ditches. Native vegetation throughout the bottom land, except near the river channel, has been almost completely replaced by farm crops.

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ECOLOGICAL RELATIONSHIPS OF THE FISH FAUNA ON CORAL REEFS OF THE MARSHALL ISLANDS¹

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INTRODUCTION

The greatly increased attention paid to scientific aspects of the central Pacific by American scientists following the close of World War II brought sharply into focus our exceedingly meager knowledge of this region. Problems faced by administrators of the

newly created Trust Territory of the Pacific, and by those responsible for maximum safety during and after atomic weapons testing operations stimulated many studies of this vast portion of the globe, of which the study reported here was a part. Significant marine problems such as the nature and distribution of the poisonous fishes of the tropical Pacific islands, the effect of nuclear explosions and radioactive con-

¹ Contribution No. 128, Hawaii Marine Laboratory, University of Hawaii.

tamination from weapons testing, and the possibility of commercial sources of marine food products required a thorough knowledge of the nature, extent, and community relationships of the marine fauna and flora. More significant, perhaps, in the long run will be the opportunity for learning more about the optima for utilizing sunlight and raw materials in this relatively isolated, but complex, ecosystem which apparently fluctuates in composition very little, if at all, from year to year, and has over a long period of time acquired a biota successfully adjusted competitively in the relatively constant environment of the tropical west-central Pacific Ocean. It has already been realized by Odum & Odum (1955) that important information might be secured on the relationship between organic productivity, energetic efficiency, and the standing crop structure of such coral reef communities. Moreover, the answers as to how steady state equilibria, such as the reef ecosystem, are self adjusted may be more easily revealed by more critical, comprehensive examination.

To reach reasonable interpretations of the energetics of production and utilization it is necessary, among other things, to determine the relationship between the standing crop, defined as the biomass of existing organisms per unit area, and productivity, defined as the rate of manufacture of this biomass per unit area (Odum 1953). Odum & Pinkerton (1955) indicate that, on a theoretical basis, systems of many types when in open steady state tend to adjust to maximum output of energy consistent with available input energy and a correspondingly low but optimum efficiency. Therefore, if the apparently steady state coral reef ecosystems tend to be similarly self adjusted regarding efficiency of energy utilization between trophic levels, and if the biota remains rather constant in composition as it certainly seems to do, then the pyramids of biomass should be roughly proportional to the standing crop for a particular coral reef area. It becomes paramount in importance, therefore, not only to know the taxonomic composition of the biota of reef areas under intensive study, but to have a rather clear concept of the biotic interaction of the species present to categorize them in proper trophic levels, and to know the community relationships in the various physiographic environments characteristic of the coral reef biotope. The importance of the type of information embodied in this paper may best be illustrated by the following statement made by Odum & Odum (1955), "Although the trophic relationships of most of the higher organisms on the reef are very imperfectly known, an attempt has nevertheless been made to make rough groupings by trophic level as to herbivores, carnivores, and decomposers."

PREVIOUS RESEARCH

Although numerous workers have reported on the feeding habits of Pacific fishes, only two authors report in any comprehensive manner and neither makes any attempt to express his results as meaningful eco-

logical aspects. In a very painstaking study of the digestive system and feeding habits of fishes of Japan, Suyehiro (1942) provided far more information on these subjects than had theretofore been available. Moreover, he included an extensive review of the literature which now makes it unnecessary to discuss this matter for the period preceding his publication. Suyehiro based his study on 88 families, 132 genera, and 150 species, providing a firm basis for many of the central Pacific families and genera. Only a few species reported by Suyehiro reach the central Pacific area. Al-Hussaini (1947) reported on a similar study of some 60 species in the vicinity of the Marine Biological Station at Ghadara, Red Sea, and included many of the widespread Indo-Pacific types. Randall (1955) reported on the fishes of the Gilbert Islands and included notes on food habits for a few of the specimens collected. Only two papers dealing with the Indo-Pacific fish fauna (Hiatt 1947a, 1947b), and these dealing with a special type of ecosystem, have approached the problem of food and feeding habits of fishes from the point of view of biotic interaction. Scattered accounts of feeding habits of Pacific fishes occur incidentally in other papers, and these will be mentioned in the species accounts where pertinent.

SCOPE OF THE PRESENT STUDY

Reported herein are accounts of the food and feeding habits and ecological relationships of 56 families of Marshallese fishes, covering 127 genera and 233 species. Some idea of the completeness of coverage of the study may be gained from the fact that in the Marshall Islands there are about 225 genera and about 600 species of fish. We have examined therefore somewhat more than half of the genera and slightly less than half of the species known to be present. Because the Marshallese fauna is part of the widespread Indo-Pacific faunal complex, the significance and applicability of this study extends a great deal further than the west-central Pacific Ocean islands.

The study was initiated at Bikini Atoll in the summer of 1947, as part of the Bikini Scientific Resurvey to determine what changes had resulted, if any, from Operations Crossroads, continued at Arno Atoll during the summer of 1950 as part of the Coral Atoll Project of the Pacific Science Board, and completed at Eniwetok Atoll during the summer of 1955 as part of the regular studies being carried out at the U. S. Atomic Energy Commission's Eniwetok Marine Biological Laboratory. The total number of individual fish stomachs examined was 2,051, of which 209 were examined at Bikini, 1,185 at Arno, and 657 at Eniwetok.

A systematic list of the families, genera, and species covered by this food study follows, and a few species, not examined for food, are cited elsewhere in the text.

ECOLOGY OF MARSHALL ISLAND FISHES

- Family Carcharhinidae (gray sharks)
Carcharhinus melanopterus (Quoy and Gaimard)
C. menisorrah (Müller and Henle)
- Family Triakidae (smooth dogfishes)
Triakodon obesus (Rüppell)
- Family Orectolobidae (carpet sharks)
Ginglymostoma ferrugineum (Lesson)
- Family Mobulidae (manta rays)
Manta alfredi (Krefft)
- Family Dussumieriidae (round herrings)
Spratelloides delicatus (Bennett)
- Family Clupeidae (sardines)
Harengula kunzei Bleeker
- Family Ophichthidae (snake eels)
Leiuranus semicinctus (Lay and Bennett)
Brachysomophis sauropsis Schultz
- Family Muraenidae (moray eels)
Echidna zebra (Shaw)
E. leucotaenia Schultz
E. polystoma (Richardson)
Uropterygius xanthopterus Bleeker
Rubulus marshallensis
 Schultz
- Gymnothorax pictus* (Ahl)
G. petelli (Bleeker)
G. javanicus (Bleeker)
G. flavimarginatus (Rüppell)
G. bueroensis (Bleeker)
G. undulatus (Lacepede)
G. margaritophorus Bleeker
G. russelli (McClelland)
G. fimbriatus (Bennett)
G. sp.
- Family Congridae (conger eels)
Conger noordziki Bleeker
- Family Moringuidae (whip eels)
Moringua macrochir Bleeker
- Family Synodontidae (lizard fishes)
Synodus variegatus (Lacepede)
Saurida gracilis (Quoy and Gaimard)
- Family Belontidae (needle fishes)
Strongylura gigantea (Temminck and Schlegel)
S. incisa (Cuvier and Valenciennes)
- Family Hemiramphidae (halfbeaks)
Hyphorhamphus laticeps (Günther)
H. affinis (Günther)
- Family Bothidae (flounders)
Bothus mancus (Broussonet)
- Family Holocentridae (squirrel fishes)
Myripristis berndti Jordan and Evermann
M. micropthalmus Bleeker
M. sp.
Holocentrus sammara (Forskål)
H. lacteoguttatus Cuvier and Valenciennes
H. microstomus Günther
H. laevis Günther
H. diadema Lacepede
H. spinifer (Forskål)
H. sp.
- Family Syngnathidae (pipe fishes)
Corythoichthys flavofasciatus conspicillatus (Jenyns)
C. intestinalis Waitei (Jordan and Seale)
- Family Aulostomidae (trumpet fishes)
Aulostomus chinensis (Linnaeus)
- Family Fistulariidae (cornet fishes)
Fistularia petimba Lacepede
- Family Atherinidae (silversides)
Stenatherina temmincki (Bleeker)
Allanetta ovalaua (Herre)
Pranesus pinguis (Lacepede)
- Family Mugilidae (mullets)
Neomyxus chaptali (Eyraud and Souleyet)
Crenimugil crenilabis (Forskål)
- Family Sphyraenidae (baracudas)
Sphyraena genie Klunzinger
- Family Polynemidae (threadfins)
Polydactylus sexfilis (Cuvier and Valenciennes)
- Family Scombridae (tunas)
Gymnosarda nuda (Günther)
Euthynnus affinis yaito Kishinouye
Katsuwonus pelamis (Linnaeus)
- Family Carangidae (jacks)
Trachurops crumenophthalmus (Bloch)
Trachinotus bailloni (Lacepede)
Carangoidea ferdau jordani Nichols
Caranx melampygus Cuvier and Valenciennes
C. lessoni Bleeker
Elagatis bipinnulatus (Quoy and Gaimard)
- Family Apogonidae (cardinal fishes)
Apogon novemfasciatus Cuvier and Valenciennes
A. snyderi Jordan and Evermann
A. exostigma (Jordan and Starks)
A. nigrofasciatus Lachner
A. novaegeinea Cuvier and Valenciennes
A. erythrinus Snyder
Apogon sp.
Gymnapogon philippinus (Herre)
Paramia quinquelineata Cuvier and Valenciennes
Cheilodipterus macrodon (Lacepede)
- Family Priacanthidae (bigeyes)
Priacanthus cruentatus (Lacepede)
- Family Serranidae (groupers)
Epinephelus merra Bloch
E. fuscoguttatus (Forskål)
E. kohleri Schultz
E. hexagonatus (Bloch and Schneider)
E. macropsilus (Bleeker)
E. spilatus Schultz
Variola louti (Forskål)
Cephalopholis urodelus (Bloch and Schneider)
C. miniatus (Forskål)
C. argus Bloch and Schneider
- Family Syngnathidae (pipe fishes)
Corythoichthys flavofasciatus conspicillatus (Jenyns)
C. intestinalis Waitei (Jordan and Seale)
- Family Aulostomidae (trumpet fishes)
Aulostomus chinensis (Linnaeus)
- Family Fistulariidae (cornet fishes)
Fistularia petimba Lacepede
- Family Pseudochromidae (trumpet fishes)
Plesiops melas Bleeker
P. nigricans (Rüppell)
Pseudogramma polyacantha (Bleeker)
- Family Pseudochromidae (tapeinomasoma)
Bleeker
- Family Pempheridae (sweepers)
Pempheris oualensis Cuvier and Valenciennes
- Family Lutjanidae (snappers)
Lutjanus monostigma (Cuvier and Valenciennes)
L. bohar (Forskål)
L. vitta (Quoy and Gaimard)
L. vaigiensis (Quoy and Gaimard)
L. gibbus (Forskål)
Scopelosus cancellatus (Cuvier and Valenciennes)
Gymnocranius griseus (Schlegel)
Lethrinus microdon Cuvier and Valenciennes
Aprion virescens Cuvier and Valenciennes
Gnathodentex aureolineatus (Lacepede)
- Family Leiognathidae (Silver perch)
Gerres argyreus (Bloch and Schneider)
- Family Sparidae (snappers)
Monotaxis grandoculis (Forskål)
- Family Mullidae (goat fishes)
Mulloidichthys samoensis (Günther)
Parupeneus trifasciatus (Lacepede)
P. barberinus (Lacepede)
P. cyclostomus (Lacepede)
Upeneus argus Jordan and Evermann
- Family Cirrhitidae (hawkfishes)
Amblycirrhitus arcatus (Cuvier and Valenciennes)
Paracirrhites forsteri (Bloch)
Cirrhitichthys aprinus (Cuvier and Valenciennes)
Cirrhitus pinnulatus (Bloch)
- Family Siganidae (rabbit fishes)
Siganus rostratus (Cuvier and Valenciennes)
- Family Kyphosidae (pilot fishes)
Kyphosus cinerascens (Forskål)
- Family Chaetodontidae (butterfly fishes)
Chaetodon lunula (Lacepede)
C. citrinellus Cuvier and Valenciennes
C. ephippium Cuvier and Valenciennes
C. vagabundus Linnaeus
C. reticulatus Cuvier and Valenciennes
C. auriga Forskål
Megaprotodon strigangulus (Gmelin)
Centropyge flavissimus
- Family Anopercidae (surgeon fishes)
Anopercodon leucogrammicus (Cuvier and Valenciennes)
Plectropomus truncatus Fowler
- Family Acanthuridae (surgeon fishes)
Acanthurus mata Cuvier and Valenciennes
A. xanthopterus Cuvier and Valenciennes
A. yahni (Forskål)
A. olivaceus Schneider
A. triostegus *triostegus* (Linnaeus)
A. achilles Shaw
A. aliale Lesson
A. nigrolineatus Cuvier and Valenciennes
A. guttatus Bloch
A. lineatus (Linnaeus)
Ctenochaetus striatus (Quoy and Gaimard)
Naso lituratus (Schneider)
N. unicornis (Forskål)
Zebrasoma veliferum (Bloch)
- Family Scorpaenidae (scorpion fishes)
Scorpaenodes parvipinnis (Garrett)
Scorpaenodes sp.
Scorpaenopsis gibbosa (Bloch)
Pterois radiata Cuvier and Valenciennes
P. volitans (Linnaeus)
Synanceja verrucosa Bloch
- Family Caracanthidae
Caracanthus unipinnus (Gray)
- Family Platyccephalidae (flatheads)
Thysanophrys sp.
- Family Pomacentridae (damselfishes)
Abudefduf sordidus (Forskål)
A. septemfasciatus (Cuvier and Valenciennes)
A. leucopomus (Lesson)
A. sazatilis (Linnaeus)
A. dickii (Lénard)
A. bicoloratus (Quoy and Gaimard)
A. amabilis (De Vis)
A. glaucus (Cuvier and Valenciennes)
A. lacrymatus (Quoy and Gaimard)
Chromis atripinnoralis Welander and Schultz
C. caeruleus (Cuvier and Valenciennes)
Dascyllus aruanus (Linnaeus)
Pomacentrus paro (Bloch)
P. nigricans (Lacepede)
P. jenkinsi Jordan and Evermann
P. albofasciatus Schlegel and Müller
P. vauvili Jordan and Seale
- Family Labridae (wrasses)
Ephibulus insidiator (Pallas)
Gomphosus varius Lacepede
Pseudocheilinus hexataenia (Bleeker)
Labroides dimidiatus (Cuvier and Valenciennes)
Novaculichthys taeniourus (Lacepede)
Stethojulis axillaris (Quoy and Gaimard)
Stethojulis sp.
Halichoeres hoeveni (Bleeker)
H. marginatus Rüppell
H. hortulanus (Lacepede)

<i>H. trimaculatus</i> (Quoy and Gaimard)	<i>Scarus bicolor</i> Rüppell
<i>H. margaritaceus</i> (Cuvier and Valenciennes)	<i>S. sordidus</i> Forskål
<i>Macropharyngodon meleagris</i> (Cuvier and Valenciennes)	<i>S. sp.</i>
<i>M. pardalis</i> (Kner)	<i>S. sp.</i>
<i>Thalassoma umbrystygma</i> (Rüppell)	<i>S. sp.</i>
<i>T. quinquevittata</i> (Lay and Bennett)	<i>Family Gobiidae (gobies)</i>
<i>T. lucasanum marnae</i> Schultz	<i>Gnatholepis anjerensis</i> (Bleeker)
<i>T. hardwickei</i> (Bennett)	<i>Gobius ornatus</i> Rüppell
<i>T. lutescens</i> (Lay and Bennett)	<i>Bathygobius fuscus fuscus</i> (Rüppell)
<i>Cheilinus oxycephalus</i> Bleeker	<i>Gobiodon erythrosipilus</i> Bleeker
<i>C. chlorourus</i> (Bloch)	<i>G. rivulatus</i> (Rüppell)
<i>C. trilobatus</i> Lacepede	<i>Paragobiodon echinocephalus</i> (Rüppell)
<i>Coris angulata</i> Lacepede	<i>Family Eleotridae (sleepers)</i>
<i>C. gaimardi</i> (Quoy and Gaimard)	<i>Valenciennea violifera</i> Jordan and Seale
<i>Hemigymnus melapterus</i> (Bloch)	<i>V. strigata</i> (Broussonet)
Family Scaridae (parrot fishes)	<i>Family Microdesmidiae</i>
<i>Cryptotomus spinidens</i> (Quoy and Gaimard)	<i>Paragobiodoides grandoculis</i> Kendall and Goldsborough

<i>S. sebae</i> (Cuvier and Valenciennes)	<i>Family Brotulidae</i>
	<i>Dinemichthys duocoeteoides</i> Bleeker
	<i>Family Balistidae (trigger fishes)</i>
	<i>Rhinecanthus rectangularis</i> (Bloch)
	<i>R. aculeatus</i> (Linnaeus)
	<i>Balistapus undulatus</i> (Mungo Park)
	<i>Balistoides viridescens</i> (Bloch and Schneider)
	<i>Pseudobalistes flavimarginatus</i> (Rüppell)
	<i>P. fuscus</i> (Bloch)
	<i>Melichthys vidua</i> (Solander)
	<i>Family Monacanthidae (file fishes)</i>
	<i>Amanes carolae</i> (Jordan and McGregor)
	<i>Oxymonacanthus longirostris</i> (Bloch)
	<i>Monacanthus</i> sp.
	<i>Family Ostracionidae (trunk fishes)</i>
	<i>Ostracion cubicus</i> Linnaeus
	<i>Family Tetraodontidae puffers)</i>
	<i>Arethron mappa</i> (Lesson)
	<i>A. hispidus</i> (Linnaeus)
	<i>A. meteagris</i> (Lacepede)
	<i>A. nigropunctatus</i> (Bloch)
	<i>Arethron</i> sp.
	<i>Family Canthigasteridae (sharp-backed puffers)</i>
	<i>Canthigaster solandri</i> (Richardson)
	<i>Family Diodontidae (spiny puffers)</i>
	<i>Diodon hystrix</i> Linnaeus

During the course of this study the authors were supported by several agencies all of which generously provided both funds, supplies, equipment, transportation, and shelter. The United States Atomic Energy Commission supported the studies at Bikini and at Eniwetok, the latter studies being carried out under the auspices of the A.E.C. Division of Biology and Medicine at the Eniwetok Marine Biological Laboratory. The study at Arno Atoll was part of the Coral Atoll Program sponsored by the Pacific Science Board of the U. S. National Research Council, under its major project Scientific Investigations in Micronesia. Funds to support the Coral Atoll Project were provided by the U. S. Office of Naval Research. Special acknowledgment is due to the Military Air Transport Service and to officials of the Civil Administrative Staff of the Trust Territory (Navy) for logistical support of this work.

The University of Hawaii through its Pacific Islands Research Fund provided generously for all the equipment and supplies for the work at Arno Atoll, and provided technical assistance in working up the mass of data collected for this study. Marian Adachi Kohn, staff artist for the Hawaii Marine Laboratory, drew the figures depicting habitat associations on the Marshallese coral reefs.

DESCRIPTION OF THE STUDY AREAS

The Marshall Islands are a group of atolls lying north of the Gilbert Islands and east of the Caroline Islands. All are enclosed in an area bounded by the parallels of latitude 4°30'N and 15°N and the meridians of longitude 161°E and 174°E (Fig. 1). They are about 2,500 statute miles west-southwest of Honolulu, Hawaii, and 4,700 statute miles from San Francisco. Most of the atolls are distributed along two chains which are nearly parallel and trend northwestward. The eastern is named the Ratak Chain (which includes Arno Atoll near its southern end)

and the western the Ralik Chain (which includes Bikini at its northern end). Besides the two main chains there are several isolated outlying atolls, of which Eniwetok Atoll is one, lying west of the chain. Bikini Atoll is located between the parallels of latitude 11°30' to 11°40'N and between the meridians of longitude 165°10' and 165°40'E. Eniwetok Atoll is located between the parallels of latitude 11°20' to 11°40'N and between the meridians of longitude 162° to 162°30'E. Arno Atoll is located between the parallels of latitude 7° to 7°30'N and between the meridians of longitude 171°30' to 172°E. The physiographic features of Bikini Atoll and Eniwetok Atoll are set forth in great detail by Emery, Tracey, & Ladd (1954), and these features for Arno Atoll were described by Wells (1951).

The major ocean current systems in the Marshall Islands area are the westerly-flowing North and South Equatorial Currents and the easterly-flowing Equatorial Countercurrent lying between them. Most of the Marshall Islands lie athwart the North Equatorial Current which extends north of latitude 6°-8°N and occupies the zone of the northeast trade winds. The Equatorial Countercurrent lies south of the North Equatorial Current and usually has its southern boundary just north of the equator. Thus Arno Atoll is located in the divergence of these current systems which brings about upwelling and resultant high organic productivity. These hydrographic conditions, coupled with a higher rainfall and resultant terrestrial productivity, make the reefs of Arno Atoll more productive than those of Bikini and Eniwetok Atolls lying farther to the north.

Water temperatures at the surface in the Marshall Islands are among the highest found anywhere in the open ocean far from large land masses. During summer average temperatures range between 82° and 85°F. The average annual range of temperature along the entire island chain down to a depth of about 300 feet is only 3° to 4°F.

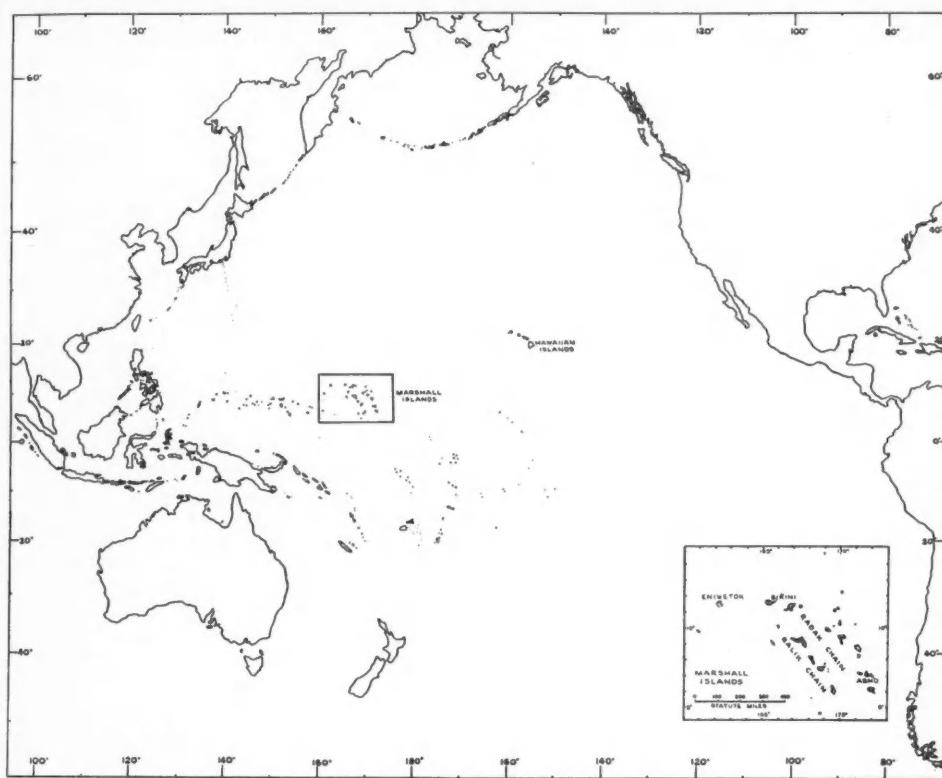


FIG. 1. The Pacific Ocean showing the location of Arno, Bikini, and Eniwetok Atolls.

Rainfall along the island chains varies considerably from north to south. At Arno the average rainfall is about 200 in, whereas at Bikini and Eniwetok it is about 50 in. The difference in rainfall is reflected in the surface oceanic salinity values which range from about 33.7 ‰ in the southern Marshall Islands to about 35.3 ‰ in the northern area of the chains. Although no data have been collected regarding tidal cycle effects on the salinity values across the reefs of Bikini and Eniwetok Atolls, such data from Arno Atoll indicate that a gradient occurs during low tides across the seaward reefs from about 50% oceanic salinity near shore to 100% oceanic salinity just off the seaward reef front. This phenomenon, associated with the runoff of fresh water from the Ghyben-Herzberg lens under the island, has a profound effect on the distribution of corals, and indirectly, if not directly, the distribution of fish on these seaward reefs (Hiatt 1958).

The tidal amplitude varies somewhat from the northern islands in the chains to those of the southern end. At Arno Atoll the mean tidal range is 3.8 ft and the mean spring tide range is about 4.1 ft. At Eniwetok and Bikini Atolls the mean tidal range is about 2.7 ft, while the mean spring tide range is about 3.9 ft. This tidal range is sufficiently extensive

to change almost completely the biotic composition of the fish fauna on the flat, table-like seaward reefs which are virtually uncovered during low tides, but which are covered by about 2-4 ft of water during high tides.

Rather detailed descriptions of the reefs of Bikini and Eniwetok Atolls are given by Tracey, Ladd & Hoffmeister (1948), Ladd, Tracey, Wells, & Emery (1950), and Emery, Tracey, & Ladd (1954). Wells (1951) has described those of Arno. Consequently, only a brief summary will be presented here. The reefs of the Marshall Islands, like those elsewhere, are highly complicated structures which can be only roughly classified into three primary types, windward, leeward, and lagoon reefs. Most of these reefs exhibit well-developed zonation, the zones tending to parallel the reef front. The nature and extent of these zones depends on many factors, e.g., prevailing winds and currents, fresh water runoff from islands, and ecological factors determining the suitability of the environment for particular species. Although no two atoll reefs are identical, the major features which are controlled by wind, waves, and temperatures, have much in common.

The windward reefs, exposed to the prevailing trades that blow from the east and northeast during

most of the year, differ markedly from the leeward reefs. The reef surface is comparatively flat and is covered with adequate water for most fishes only during periods of high tides. The outer marginal zones are usually flourishing and most often are bordered by a coralline ridge which receives the main impact of the waves. These reefs flats may be up to a half-mile in width, with several distinctive shoreward zones in which characteristic faunal and floral associations appear.

The leeward reefs are narrow, being only 200-500 ft in width. Their seaward margins are usually made irregular by surge channels which frequently extend inward 10-30 yds. No coralline ridge is present, and corals grow in great profusion, covering half or more of the reef surface. Usually, the leeward reefs are less elevated than those of the windward type so that the biota is resident. Only the largest of the roving carnivores slip over the reef front at high tide to forage on the reef flat.

Lagoon reefs vary depending upon their exposure to the prevailing wind. In protected areas there is a discontinuous series of irregular reef patches which extend from near shore to the outer slope leading to the deeper parts of the lagoon. These reef patches are not subjected to heavy wave impact, the only water movement aside from prevailing currents which affects them is the slow ocean swells which enter the lagoons through passages. Usually these conditions favor a luxuriant growth of coral in its more delicate form, imparting to these coral patches striking beauty. The fauna and flora are largely unaffected by tides and remain closely associated with the coral patches. Extensive sand and rubble flats separate the coral patches, and characteristic animal communities there contrast with those ecologically more closely tied to coral patches. On the leeward side of these atolls the lagoon reefs are better developed and frequently are continuous, because they receive fairly strong waves engendered by the prevailing winds which have a fetch of up to 20 miles or more across the lagoon. In some instances, these reefs come to resemble those characteristic of the windward side of the atoll, in that they frequently have an elevated algal ridge bordering the reef margin and may be flattened shoreward of the reef margin. However, they usually lack the distinct zonation characteristic of the seaward reefs of the windward side.

METHODS

Most of the fishes collected for this study were taken by poisoning sections of the reefs with rotenone. However, many were taken with spears, hook and line, explosives, and other techniques suitable for the occasion. The advantage of rotenone is that it almost simultaneously kills all fish in an area, and causes those deep in interstices of the corals and rocks, as well as those in burrows to come to the surface. In this way all members of a fish community can be collected and analyzed for their interrelationships as all niches filled give up their fish fauna for study.

The following data were recorded for each specimen examined: (1) standard length, (2) sex, (3) extent of development of the gonads, (4) nature of the alimentary tract, i.e., length, thickness of intestinal wall, presence or absence of a gizzard, (5) nature of the dentition and gill rakers, position and special features of the mouth, and (6) type of food items contained in the stomach, or, if empty, those found in the intestine.

For the food habits analysis the particular food items were listed and the numbers of fish containing the items were tallied. This method was used because it gives essentially the predilection of each fish species for particular items of diet. In studies of food and feeding interrelationships these types of data are most important. Such methods of analysis as the comparative quantities of different food items ingested become significant only when sufficient specimens are analyzed to ensure that one or a few large items taken by only one or a few fish do not give spurious percentages for the total. In most cases in the present study neither time nor specimens were available to add biomass or volume measurements. However, in those instances when a fish had consumed a great preponderance of a particular item, along with numerous other incidental items, it was noted in our records. For many species sufficient specimens were examined so that the percentage of fish containing the item became significant, and these are so listed in the systematic analysis of the food and feeding habits. If too few fish were available the results were recorded simply as the number of fish containing the item.

Naturally, collecting fish by means of rotenone poisoning resulted in many of the large carnivorous and predaceous species consuming smaller species which had succumbed earlier to the poison. Fish found in the stomachs which appeared too freshly caught were therefore discarded.

It will be obvious to the reader that biotic interrelationships and community groupings based solely on circumstantial evidence presented by food items in stomachs and structural features adapted for food getting, while exceedingly important, could not provide all the evidence needed to interpret data such as are presented in this paper. Consequently, it will be reassuring to state that hundreds of hours of underwater observations using skin-diving equipment have contributed very substantially to our results and interpretations. As a matter of fact, the analyses of natural aggregations in the various habitats on the reefs, to be presented later in this paper, were only possible by combining our field observations with the stomach analyses.

The results of our studies will be presented first by a systematic analysis and discussion of the food and feeding habits of the species, genera, and families represented. Following these data an analysis will be made of the major feeding habits characteristic of the species studied. Discussions will include such natural groupings as algal feeders, plankton feeders,

omnivores, detritus feeders and scavengers, coral polyp feeders, and large roving carnivores. The interrelationships of naturally occurring assemblages on the reefs will be discussed also. In this section accounts will cover fish associated with mid-water and surface fauna, fish associated with the bottom, fish associated with rock and coral ledges and caverns, fish associated with branching corals and their dead bases, fish associated with solid coral heads, fish

associated with the surf zone, fish associated with the windward sea reef flats, and fish associated with tide pools.

Discussions of the trophic levels represented by the fish studied will be presented also. Following this section the study will be summarized by a consideration of the results in the form of the food chains and the food web found on these coral reefs of the Marshall Islands.

FOOD AND FEEDING HABITS BY TAXONOMIC CATEGORIES

Family Carcharhinidae

Species: *Carcharhinus melanopterus* (black-tipped shark)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: 1 male; 1 female
Standard length: 690-1,200 mm

Two specimens were caught near the garbage dump; one stomach was empty and one contained garbage only. One specimen taken on the seaward reef flats had a partly digested fish in its stomach. This is the most common shark on the seaward reefs both on the windward and leeward sides of the atolls. It moves onto the reef flat as the tide rises, and forages widely. It also occurs on the lagoon reefs, but there the individuals are usually of larger size and are less numerous than on the seaward reefs. This shark seems to have a rather curious nature and many encounters with it in the water indicate that it has poor vision. Consequently, it usually approaches very closely to persons wading or swimming before it suddenly darts away. It habitually enters recently poisoned areas to devour small fish rendered moribund by rotenone, and is itself rather resistant to this poison. It is classed as a roving carnivore and scavenger.

Species: *C. menisorrah* (gray shark)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 1,450 mm

One specimen was caught at the garbage dump, but the stomach was empty. This species is more common in the lagoons than is *C. melanopterus*, and is also found along the outer edge of the seaward reef front cruising in water 15-20 ft in depth. It frequently enters surge channels along the seaward reef. On numerous occasions this species has competed with us in picking up fish during poison station operations. At such times, individuals up to 7-8 ft in length enter water only 2-3 ft deep. It is classed as a roving carnivore and scavenger.

Family Summary

Members of the Family Carcharhinidae are by far the most abundant sharks on Marshallese reefs, and certainly occupy an important position among the carnivores as well as the scavengers of the coral reef community.

Family Triakidae

Species: *Triakodon obesus* (white-tipped shark)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 1,150 mm

One specimen caught near the garbage dump had no food in its stomach. Next to *C. melanopterus* this shark is the most abundant on Marshallese reefs both in the lagoon and in lee seaward reefs. It is ubiquitous in surge channels and competes lively in picking up fish

killed by rotenone. It is not timid and approaches disconcertingly close to humans before turning away. As with *C. melanopterus*, its vision seems to be poor and its apparent boldness is probably just exploratory.

Family Orectolobidae

Species: *Ginglymostoma ferrugineum* (nurse shark)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Males and females
Standard length: 2,100-2,500 mm

Two of the specimens were empty and the third contained partly digested remains of a rabbit fish (*Siganus* sp.). Since the nurse sharks were taken near the garbage dump, it is probable that the *Siganus* may have been dead before it was eaten. The species is a very sluggish, bottom-dwelling scavenger which rarely comes into water less than 50 ft deep. It was never seen on the reefs by us in the Marshall Islands, but a small individual was taken in shallow water in the Gilbert Islands.

Family Mobulidae

Species: *Manta alfredi* (manta ray)
Number examined: Bikini, 1 specimen
Sex: Female
Standard breadth: 2,950 mm

The stomach of this specimen contained approximately one quart of copepods and other crustacean plankters. Its planktonic feeding habits are well known. These rays were seen daily swimming about near the center of Enyu Channel, Bikini, and occasionally at various other places at Eniwetok and Arno. At Arno one approached us very closely while we were swimming just seaward of the reef margin near Ine Village, coming to within 20-30 ft of the reef edge.

Family Dussumieriidae

Species: *Spratelloides delicatulus* (round herring)
Number examined: Arno, 20 specimens
Sex: Both males and females
Standard length: 20-70 mm
Digestive tract: Gill rakers very long; Y-shaped stomach; short, straight intestine.

Food item	Percentage of fish containing the item
Crustacea	
Copepods	85
Shrimp larvae	80
Ostracods	50
Crab zoeae	20
Mollusca	
Protoconchs	10
Polychaeta	10

This species is a typical plankton feeder, and shows a strong predilection for planktonic crustaceans. It occurs at all three atolls in very large schools on the lagoon reefs and on sheltered seaward reefs, occurring even in very shallow water just off the beaches. It is

especially common around piers and ships' hulls. Tunas, belonids, and the carangid, *Scomberoides sanctipetri*, frequently are seen slashing through these dense schools of round herrings. Terns hover above the schools to catch the fish whenever they swim close to the surface.

Family Clupeidae

Species: *Harengula kunzei* (sardine)
Number examined: Arno, 20 specimens
Sex: Both males and females
Standard length: 37-82 mm.

Digestive tract: Y-shaped stomach; straight, short intestine

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	55
Ostracods	50
Copepods	15
Shrimp larvae	10
Unidentified crustacean fragments	40
Polychaeta	15
Foraminifera	
<i>Calcarina</i> sp.	5

This species, seen only at Arno, occurred in large schools in shallow water near the lagoon beaches. Unlike its counterpart in Japan, *H. zunasi*, which is exclusively a plankton feeder (Suyehiro 1942) taking diatoms and copepods, the Arno species is carnivorous and feeds on the shallow bottom fauna.

Family Ophichthidae

Species: *Leiuranus semicinctus* (snake eel)
Number examined: Eniwetok, 5; Bikini, 1 specimen: 5 empty
Sex: Undeveloped
Standard length: 215-490 mm
Digestive tract: short, straight intestine

The single specimen with food in its stomach contained a partly digested fossorial hemichordate, *Ptychoderma* sp. It apparently feeds under the sand where it is common in areas of fine gravel-like deposits on the shallow reefs. It does not live in permanent burrows, but is capable of burying itself rather rapidly.

Species: *Brachysomophis sauropsis* (snake eel)
Number examined: Eniwetok, 2 specimens
Sex: Males
Standard length: 260-400 mm
Digestive tract: short, straight intestine

The food found in these two specimens consisted of unidentified fish fragments, a very small *Octopus* sp., several specimens of the ubiquitous foraminiferan, *Calcarina* sp., and sand grains. Like *L. semicinctus*, this species lives buried in gravelly sand without permanent burrows. It was taken commonly on all reef areas where sandy bottoms occurred. Unlike *L. semicinctus*, which has the eyes normally located on the head, *B. sauropsis* has the eyes almost at the tip of the snout, which, together with the food items taken, suggests that the latter species probably lies under the sand with just the tip of the snout protruding, keeping watch for prey inadvertently crawling or swimming close to it.

Family Muraenidae

Species: *Echidna zebra* (moray eel)
Number examined: Arno, 2 specimens
Sex: Male
Standard length: 375-575 mm
Digestive tract: teeth molariform; short, straight intestine

The specimens examined had all consumed crabs of the genus *Eitisus* and other unidentified xanthids, and one contained, in addition, the crushed shell of the common reef urchin, *Echinometra mathaei*.

Species: *Echidna leucotaenia* (moray eel)

Number examined: Arno, 2 specimens

Sex: Male

Standard length: 365 mm

Digestive tract: Teeth molariform; short, straight intestine.

The specimens examined had crab fragments in their stomachs; one had fragments of a swimming crab (Portunidae) and the other contained fragments of a xanthid crab.

Species: *Echidna polyzona* (moray eel)

Number examined: Eniwetok, 1 specimen

Sex: Undeveloped

Standard length: 520 mm

Digestive tract: Teeth molariform; short, straight intestine

This specimen had consumed a large shrimp, *Saron marmoratus*, which habitually secludes itself under rocks and ledges.

Generic Summary

None of the species of *Echidna* is common, but some specimens are usually collected in extensive poison stations. All live very secretly in crevices or under rocks on the shallow reefs and are almost never seen by skin-divers. Structurally unique in this genus is the extensive, flattened, cobble-like dentition well adapted for crushing, rather than the shearing and stabbing teeth found in other genera of moray eels. Their prey is apparently seized as it crawls into or near the crevices in which the morays lie concealed. The sea urchin taken by one specimen is a rock dwelling species which usually is difficult to extricate from its tightly fitting depression.

Species: *Uropterygius xanthopterus* (moray eel)

Number examined: Arno, 8 specimens; 4 empty

Sex: Males and females

Standard length: 187-315 mm

Digestive tract: Teeth conical, pointed, canine-like; short straight intestine.

All four eels with food had crustacean fragments only. Three contained xanthid crab fragments and three contained alpheid shrimp fragments. This eel lives in interstices of coral mounds and masses of coralline rubble. It is strongly demersal and seldom is seen outside its place of refuge.

Species: *Rabula marshallensis* (moray eel)

Number examined: Arno, 2 specimens

Sex: Male and female

Standard length: 147-159 mm

Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Both specimens contained fragments of small crabs. This moray lives in interstices of coral mounds and rocky debris.

Species: *Gymnothorax pictus* (moray eel)

Number examined: Arno, 4; Eniwetok, 2: 2 empty

Sex: Males and females

Standard length: 400-725 mm

Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Of the four fish having food in their stomachs three had unidentified fish fragments and two had small crab fragments. This is the common moray found near the beach under rocks on the seaward reef flats. It is frequently encountered moving about reefs exposed by the receding tide, and commonly secludes itself under the nearest rock when startled by waders. Often it mistakes the shoes of the intruder for a rock and tries to seclude itself there, most often unsuccessfully, because humans can outrun it. Like most morays, it is vicious when teased with a stick.

Species: *Gymnothorax petelli* (moray eel)
 Number examined: Arno, 14; Bikini, 1 specimen: 13 empty
 Sex: Males and females
 Standard length: 108-520 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, heavy-walled, straight intestine

Each of the two specimens containing food had crab fragments, while one had, in addition, a hippolytid shrimp, and the other contained a partly digested small fish, *Pomacentrus jenkinsi*. This comparatively small moray has habits similar to most of the others. However, it seems clear that it must feed predominantly at night, because of the small proportion of those with food in their stomachs to those without.

Species: *Gymnothorax javanicus* (moray eel)
 Number examined: Arno, 4 specimens: 2 empty
 Sex: Undeveloped
 Standard length: 102-287 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

One of the two specimens containing food items had an alheid shrimp, and the other contained fragments of unidentified gobies. This moray attains a very large size, some of those observed having a length of 6-7 ft. Like other morays it is seldom seen on the reefs because of its habit of secreting itself in interstices of large coral heads and coral rubble. When observed while skin-diving this eel usually has the head and forepart of the body extended from its hiding place. It is probably a night feeder.

Species: *Gymnothorax flavimarginatus* (moray eel)
 Number examined: Arno, 9; Eniwetok, 2 specimens: 7 empty
 Sex: Males and females
 Standard length: 185-690 mm
 Digestive tract: Conical, pointed, canine-like teeth; short, straight intestine

Only four of the 11 specimens examined contained food. In two of them, crab fragments were found; fragments of a blenny (*Cirripectes variolosus*), a damsel fish (*Abudefduf dicki*), and other unidentified species of fish were found in three of them. The habits of *flavimarginatus* are similar to those of *G. javanicus*, and like the latter, it also attains large sizes.

Species: *Gymnothorax bueroensis* (moray eel)
 Number examined: Arno, 21; Eniwetok, 4 specimens: 8 empty
 Sex: Males and females
 Standard length: 125-310 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments, unid.	64
Xanthid crab fragments	11
<i>Trapezia</i> sp.	5
Shrimp fragments	8
Stomatopod fragments	5
Fish	
Fish fragments, unid.	5
Labrid, unid.	5

This is the most abundant moray on the reefs of the Marshall Islands. It is a comparatively small species which has habits similar to other morays as regards seclusion and feeding habits.

Species: *Gymnothorax undulatus* (moray eel)
 Number examined: Eniwetok, 6 specimens: 4 empty
 Sex: Males and females
 Standard length: 600-700 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Only two of these specimens contained food items, and these were small pomacentrids and labrids which

undoubtedly had succumbed earlier to the rotenone. Like most other morays, this species probably feeds at night. It is very large and seems especially vicious. Its habits are similar to the other morays.

Species: *Gymnothorax margaritophorus* (moray eel)
 Number examined: Eniwetok, 8 specimens: 4 empty
 Sex: Females and undeveloped
 Standard length: 160-420 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Of the four specimens containing food, two had only gurry, another contained crustacean fragments, and the fourth contained unidentified fish fragments. This common species of the interisland reefs and seaward reef shallows does not grow large. It frequently may be found in the interstices of dead coral heads.

Species: *Gymnothorax rupelli* (moray eel)
 Number examined: Eniwetok, 4 specimens: all empty
 Sex: Females and undeveloped
 Standard length: 300-550 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

The lack of food in the stomachs examined probably indicates a night feeding habit. However, this species appears to have habits similar to other comparatively small morays, so it doubtless feeds on crustaceans and small fish. It is particularly common on the seaward reef flats and on the interisland reefs where it hides in any crevice or under any rock available.

Species: *Gymnothorax fimbriatus* (moray eel)
 Number examined: Eniwetok, 1 specimen: empty
 Sex: Undeveloped
 Standard length: 250 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

This moray is especially common in coral heads on the interisland reefs and leeward seaward reefs. It is a small species, frequently found when cracking open coral heads carried ashore. Its digestive tract and teeth indicate that it feeds like the other members of the genus.

Species: *Gymnothorax* sp. (moray eel)
 Number examined: Bikini, 14 specimens: 7 empty
 Sex: Males and females
 Standard length: 230-700 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Food item	Percentage of fish containing the item
Crustacea	
<i>Odontodactylus</i> sp.	28
Xanthid crabs, unid.	28
<i>Elysia</i> sp.	14
Fish	
<i>Siganus rostratus</i>	14
<i>Abudefduf leucopomus</i>	14
Unid. fragments	14
Foraminifera	
Foraminiferans and sand	14

This large moray apparently feeds also mostly by night, but a sufficient number contained food to indicate that its food and feeding habits are similar to the other morays.

Family Summary

Except for the genus *Echidna* the moray eels have very similar habits of concealment and food getting. A few become very large and are certainly the most vicious of the reef fishes, although, if unprovoked, will do little more than watch human intruders, with the head and forepart of the body protruding from a hole or crevice in the reef. Crustaceans appear to be the

food type most frequently taken, doubtless because these crustaceans, like the eels, become active at night and leave their diurnal hiding places in crevices and under the sand to forage. Moray eels appear to be predominantly night feeders, as judged by the high proportion of them without food in their stomachs during the day. Small fish species which habitually remain close to coral heads and rubble are also taken commonly. The kinds of food items found suggest that morays do not forage widely, but apparently catch their prey by watchful waiting methods.

An observation made in Hawaii indicates that morays are also adept at stalking prey. One swam slowly along the edge of a rocky pool watching a lined shore crab, *Grapsus grapsus tenuicrustatus*, walking along the rock about two feet above the water's surface. Suddenly the moray slithered up the rock in pursuit of the crab, caught it and fell back into the water. Likewise, the actions of *G. pictus* slithering along on just a film of water on the seaward reef flats suggest that it seeks prey both in and out of the water.

The fang-like canine teeth, some of which are depressible, are admirably suited to predacious habits.

Family Congridae

Species: *Conger noordziki* (conger eel)
Number examined: Arno, 4; Bikini, 1; Eniwetok, 1 specimen:
1 empty
Sex: Males and undeveloped
Standard length: 151-620 mm
Digestive tract: Teeth short, conical, very numerous and point backwards; stomach elongate, Y-shaped; intestine short, and nearly straight

Each specimen contained different food items among which were shrimp fragments, unidentified crustacean fragments, polychaete worms, unidentified fish fragments, and fish eggs. Like other eels, the conger is cryptic and is seldom seen during the day. Its night feeding forays were observed several times when the eels came into very shallow water seeking prey.

Family Moringuidae

Species: *Moringua macrochir* (whip eel)
Number examined: Arno, 20; Eniwetok, 2 specimens: 12 empty
Sex: Males and females
Standard length: 128-260 mm
Digestive tract: Short, straight intestine

Food item	Percentage of fish containing the item
Polychaeta	60
Foraminifera	
<i>Calcarina</i> sp.	40
Fish	
Unid. fragments	10
Sand	30

The whip eels are quite common in sandy bottoms of the reefs shallows on all atolls. They construct no permanent burrows, but lie below the sand completely out of sight during the day. Whip eels apparently forage for prey species just under the sand and on the bottom.

Family Synodontidae

Species: *Synodus variegatus* (lizard fish)
Number examined: Arno, 8; Bikini, 4; Eniwetok, 5 specimens:
10 empty
Sex: Males and females
Standard length: 72-220 mm
Digestive tract: Teeth canine-like, numerous on both jaws and tongue; stomach heavy-walled; intestine short, straight

Food item	Percentage of fish containing the item
Unid. fragments	71
<i>Epinephelus</i> sp.	14
<i>Abudedefduf</i> sp.	14

Five specimens collected at Eniwetok had picked up recently poisoned fish and were considered as empty for this study. This species is ubiquitous on sandy patches in all reefs areas. It lies mostly buried in the sand, with only the eyes and forepart of the head exposed watching for prey which may venture too closely. It is obliteratively colored for sandy bottom, so that its habit of lying perfectly motionless until it darts out after its victim is very effective. It is a voracious, small carnivore.

Species: *Saurida gracilis* (lizard fish)

Number examined: Arno, 16 specimens: 4 empty

Sex: Males and undeveloped

Standard length: 45-131 mm

Digestive tract: Teeth canine-like in profusion on both jaws, palatines, vomer, and tongue; teeth on jaws not covered by lips; stomach heavy-walled; intestine short, straight

Food item	Percentage of fish containing the item
Unid. fragments	67
Unid. juvenile fish	17
<i>A pogon novemfasciatus</i>	8
<i>Allanetta ovalaua</i>	8
Fish scales	8

This species is distributed widely about all reefs, and has habits very similar to *Synodus variegatus*.

Family Summary

Lizard fish have obliterative color patterns so that when they lie motionless on sandy bottoms, or are partially buried in the sand, they are virtually impossible to detect. When prey species, mostly small fish, come within a few feet of them they dart upward very rapidly and seize their victim. Rarely have they been observed to swim more than 3-4 ft upward while attacking prey species. The profuse and powerful canine-like dentition provides a very effective mechanism for catching small fish. Our analyses and observations indicate that only fish were taken as food. However, Suyehiro (1942) reports that *Saurida undosquamis* in Japan will take shrimps and squid in addition to its more usual diet of small fish.

Family Belonidae

Species: *Strongylura gigantea* (needle fish; "Gar fish")

Number examined: Eniwetok, 2 specimens: both empty

Sex: Male and female

Standard length: 840-1,030 mm

Digestive tract: Jaws extremely long and needle-like toward the tip, mouth large, teeth canine-like arranged in villiform bands with inner row of enlarged canines; alimentary tract a straight, heavy-walled tube divided into an oesophagus and intestine, no stomach.

Both specimens examined had been caught by hook and line near the garbage dump, and one contained only garbage in its stomach. Observations indicate that this surface swimming species is a voracious carnivore, feeding on small fish by drifting up to them and then suddenly lashing out with its jaws.

Species: *Strongylura incisa* (needle fish)

Number examined: Arno, 1 specimen

Sex: Undeveloped

Standard length: 143 mm

Digestive tract: Jaws and teeth similar to *S. gigantea*; alimentary tract a straight tube, no stomach.

This specimen, a very small one, contained a small fish, *Allanetta ovalaua*.

Family Summary

Members of the Family Belonidae apparently feed by drifting into schools of fish or crustaceans (Randall 1955), whereupon they suddenly lash out with their

long, tooth-lined jaws to capture their prey. In our observations, and in those of Al-Hussaini (1947), small schooling species such as round herrings and silversides were most often the object of these carnivores which travel in small schools just below the surface. However, Suyehiro (1942) mentions that a closely related species in Japan, *Athlennes anastomella*, contained the remains of a rather large fish. Japanese fishermen also report that this species uses its long, powerful jaws very effectively in attacking larger prey species.

Family Hemiramphidae

Species: *Hyporhamphus laticeps* (halfbeak)
Number examined: Bikini, 8; Eniwetok, 12 specimens: 1 empty
Sex: Males and females
Standard length: 215-320 mm
Digestive tract: Lower jaw elongate and pointed, upper jaw short, teeth in both jaws minute, mouth large; a straight tube from the oesophagus to the anus, no stomach

Food item	Percentage of fish containing the item
Fish	
Unid. small fish (probably round herrings)	47
Crustacea	
Shrimp larvae	21
Mysids	15
Shrimp fragments	10
Crab zoeae	5
Polychaeta	
Unid. swimming polychaetes	26

This species swims in midwater or near the surface in small schools on all reefs investigated. It is a small, midwater carnivore which feeds on whatever prey species are available, showing comparatively little predilection for small fish species over swimming crustaceans or polychaetes.

Species: *Hyporhamphus affinis* (halfbeak)
Number examined: Arno, 16 specimens: 3 empty
Sex: Unknown
Standard length: Unmeasured
Digestive tract: Similar to *H. laticeps*

Food item	Percentage of fish containing the item
Crustacea	
Copepods	30
Crab zoeae	23
Crab fragments	15
Fish	
Unid. fragments	30
Foraminifera	
Several pelagic species	30
Gastropoda	
Veliger larvae	8
Gurry	23

This species apparently feeds predominantly on plankton, but it is capable also of taking small fish.

Family Summary

The halfbeaks are comparatively small, mid-water and surface dwellers where they occur in rather large schools. Younger individuals are primarily zooplankton feeders, but as they become larger their predilection turns to small, densely schooling surface fishes such as round herrings and silversides.

Earlier accounts (Jordan 1907) suggest that the halfbeaks are phytoplankton feeders, but this seems to be in error as our studies, as well as those of Uehida, reported by Suyehiro (1942), indicate that they are carnivores. No particular function can be ascribed to the elongate lower jaw by us, although it may be used to stun small fishes by a slashing action. Uehida believes that not only is the lower jaw useless when taking food, but actually is a hindrance.

Family Bothidae

Species: *Bothus mancus* (flounder)
Number examined: Arno, 5; Bikini, 6; Eniwetok, 12 specimens: 4 empty
Sex: Males and females
Standard length: 97-300 mm
Digestive tract: Short, nearly straight intestine

Food item	Percentage of fish containing the item
Fish	
Unid. gobies	21
Unid. fragments	21
<i>Acanthurus t. triostegus</i> (juvenile)	10
Unid. labrid (juvenile)	10
Unid. labrid	10
<i>Parupeneus trifasciatus</i>	5
<i>Ctenogobius</i> sp.	5
<i>Abudefduf amabilis</i>	5
Pomacentrid (juvenile)	5
<i>Apogon novemfauciatus</i>	5
<i>A. erythrinus</i>	5
<i>Istiblennius pavlus</i>	5
<i>Tripterygion minutus</i>	5
Crustacea	
<i>Odontodactylus</i> sp.	15
<i>Trajezia</i> sp.	10
<i>Thalamita</i> sp. fragments	10
Portunid fragments	5
Xanthid crab fragments	5
Palaemonid shrimp fragments	5
Amphipod	5

With a very effective obliteratively colored upper surface this flounder lies motionless on rocks or sandy bottoms on all reefs studied. At times it covers itself, except for the eyes, with sand, thus becoming almost impossible to discern. After thus lying in wait for prey species to venture close enough, it seizes any fish or crustacean possible for it to ingest. Insofar as we could ascertain it responds only to moving prey. All the food items taken are species which frequent the bottom in sandy areas adjacent to coral mounds or rubble.

Family Holocentridae

Species: *Myripristis berndti* (squirrel fish)
Number examined: Arno, 7 specimens: 2 empty
Sex: Females and undeveloped
Standard length: 40-99 mm
Digestive tract: Teeth short, rather weak; stomach moderately heavy-walled; intestine short, straight

All five of the specimens containing food had only fragments of shrimps. This species and all other holocentrids examined had very little food in their stomachs, which is to be expected, since they are well known night feeders. All specimens of this species examined by Randall (1955) in the Gilbert Islands were empty of food.

Species: *Myripristis microphthalmus* (squirrel fish)
Number examined: Eniwetok, 17 specimens: 5 empty
Sex: Males and females
Standard length: 135-170 mm
Digestive tract: Similar to *M. berndti*

Food item	Percentage of fish containing the item
Crustacea	
Unid. crab fragments	58
Portunid crabs	16
Crab megalopa	8
Crab zoeae	8
Unid. shrimps	25
Alpheid shrimp	8
Stomatopod fragments	16
<i>Galathea</i> sp.	8
Amphipods	8
Polychaeta	
Unid. tube dwellers in sand near coral mound	16
Algae	
<i>Turbinaria</i> sp. tips	8
Sand grains	8

This species takes a great variety of crustaceans which are associated with, or swim near, the coral mounds in which this spelean fish secludes itself. Two specimens had the gut filled with hundreds of polychaetes which inhabit membranous tubes forming a dense network just beneath the surface of the rather compacted sandy bottoms on the protected lagoon reefs. The lack of sand in the gut indicates that the worms were pulled from their tubes, rather than being excavated from the sand by rooting actions of the fish.

Species: *Myripristis* sp. (squirrel fish)
Number examined: Bikini, 7 specimens: 5 empty
Sex: Males and females
Standard length: 70-210 mm
Digestive tract: Similar to *M. berndti*

Stomach contents of the two specimens containing food consisted of the following crustaceans: *Odontodactylus* sp., inachid crab fragments, and amphipods; and the following small fish: *Ctenochaetus striatus*, labrids, and unidentified larval stages.

Species: *Holocentrus sammara* (squirrel fish)
Number examined: Arno, 5; Eniwetok, 8 specimens: 2 empty
Sex: Males and females
Standard length: 34-165 mm
Digestive tract: Teeth short, weak; stomach moderately heavily-walled; intestine medium in length with one loop.

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	36
Parthenopid crab	27
<i>Thalamita</i> sp.	18
<i>Pachygrapsus plicatus</i>	9
Portunid crab	9
Maill crab	9
Unid. crustacean fragments	18
Copepods	9
Coelenterata	
Pieces of unid. coral, partly digested	18
Polychaeta	
Unid. polychaetes	9
Gastropoda	
<i>Cerithium</i> sp.	9
Algae	
Algal frond, bitten off	0

This species, like other squirrel fish, hides under rocks or in small coral caverns during the day, and feeds primarily at night. However, it is the most commonly observed squirrel fish during the day, as it frequently comes out of its hiding place and seems less secretive than the others.

Species: *Holocentrus lacteoguttatus* (squirrel fish)
Number examined: Arno, 4 specimens: 1 empty
Sex: Females
Standard length: 59-82 mm
Digestive tract: Similar to *H. sammara*

Shrimp fragments, small gastropods, and gurry were found in the three specimens containing food in their stomachs.

Species: *Holocentrus microstomus* (squirrel fish)
Number examined: Arno, 24; Eniwetok, 5 specimens: 3 empty
Sex: Males and females
Standard length: 45-191 mm
Digestive tract: Similar to *H. sammara*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	42
Shrimp fragments	23
Alheid shrimp	6
<i>Gonodactylus</i> sp.	3
Fish	
Unid. fragments	15
<i>Chromis caeruleus</i>	3

Gastropoda	
Small unid. gastropods	3
Coelenterata	
Hydroid fragments	3
Polychaeta	
Unid. polychaetes	3
Gurry	6

Species: *Holocentrus laevis* (squirrel fish)
Number examined: Eniwetok, 4 specimens: 1 empty
Sex: Males and females
Standard length: 125-150 mm
Digestive tract: Similar to *H. sammara*

In the three fish containing food in their stomachs the following crustaceans were found: crab fragments, a portunid crab, a maill crab, and shrimp fragments.

Species: *Holocentrus diadema* (squirrel fish)
Number examined: Eniwetok, 14 specimens: 1 empty
Sex: Males and undeveloped
Standard length: 75-120 mm
Digestive tract: Similar to *H. sammara*

Food item	Percentage of fish containing the item
Gastropoda	
<i>Atys</i> sp.	46
Unid. gastropods	14
Polychaeta	
Unid. polychaetes	46
Crustacea	
Xanthid crab fragments	38
Isopods	23
Unid. fragments	14
Shrimp fragments	7
Alheid shrimp	7
Pelecypoda	
Small coral-dwelling clams	14
Amphineurs	
<i>Solenostomus</i> sp.	7

Species: *Holocentrus spinifer* (squirrel fish)
Number examined: Eniwetok, 9 specimens: 1 empty
Sex: Males and females
Standard length: 150-280 mm
Digestive tract: Similar to *H. sammara*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crabs	50
<i>Charcydium</i> sp.	12
Portunid crab	12
Maill crab	12
Stomatopod	12
Fish	
Unid. fragments	12

Species: *Holocentrus* sp. (squirrel fish)
Specimens examined: Bikini, 5 specimens
Sex: Males and females
Standard length: 80-140 mm
Digestive tract: Similar to *H. sammara*

Three of the five specimens contained only fragments of the small coral crab, *Trapezia* sp., while the remaining two specimens contained only shrimp fragments.

Family Summary

Food and feeding habits of all members of this family appear to be very similar. All are carnivores, taking a wide variety of crustaceans, polychaetes, small fish, and gastropods. During the day squirrel fish are cryptic, secluding themselves to a great extent in holes, under ledges, or in larger caverns in coral mounds or rubble. All have comparatively large eyes, and feed almost exclusively at night. Food remains are infrequent in the stomachs during the day, persistent items being generally the hard parts of prey taken the previous night. In many instances the intestines had to be searched for traces of food items because the stomachs were empty. Randall (1955) reported that most of the stomachs of holocentrids in the Gilbert Islands were

also empty, and those containing food had remains of crustaceans and small fish.

The fact that many of the squirrel fish contained polychaetes which were tube dwellers on sandy bottoms indicates that they do forage well away from their day time hiding places. None were observed feeding on these polychaetes during daylight hours. Further evidence of their foraging on sand bottoms is shown by the presence of sand dwelling gastropods (*Atys* sp.) and the fossorial solenogastrid amphineurans. The few broken, partly digested tips of coral branches in the stomach of *H. sammarus* may have been taken inadvertently while the fish was seeking small crabs wedged in interstices. We do not believe that any holocentrid feeds habitually on living coral.

Family Syngnathidae

Species: *Corythoichthys flavofasciatus conspicillatus* (pipefish)
Number examined: Eniwetok, 3 specimens
Sex: Males and females
Standard length: 82-95 mm
Digestive tract: Snout long, pipette-like; mouth cavity small, teeth absent; alimentary canal straight, no stomach.

All three pipefish examined contained copepods; one had, in addition, some small isopods, and another had taken several ostracods along with the copepods. This pipefish is very common on all reefs studied in the northern Marshalls, and frequently is seen lying on coral heads, rubble, or sand.

Species: *Corythoichthys intestinalis waitei* (pipefish)
Number examined: Arno, 1 specimen
Sex: Female
Standard length: 85 mm
Digestive tract: Similar to *C. f. conspicillatus*

This specimen contained copepods, copepod nauplii, and ostracods in about equal abundance. Although this pipefish was not seen at either Eniwetok or Bikini, it was locally abundant at Arno and Majuro Atolls in the southern Marshalls. Its habits are very much like those of *C. f. conspicillatus*.

Generic Summary

The food getting structures and the food items eaten by the two species of *Corythoichthys* suggest that these pipefish probably use their snout as a sort of pipette to take up minute crustaceans so abundant on the surface of coral rubble and compacted sand bottoms. Al-Hussaini (1947) suggests that the pipefishes take mostly planktonic crustaceans, but we believe that the species ingested are benthonic. There is no evidence that the snout is distensible or that they can swallow prey larger than might be expected, as Bigelow & Welsh (1924) have described for the related species *Siphonostoma fuscum* of the east coast of North America.

Family Aulostomidae

Species: *Aulostomus chinensis* (trumpet fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 600 mm
Digestive tract: Snout very long, tubular, with jaws at end, mouth capable of bellows-like dilation; intestine short, straight

The single specimen examined was taken by spear, and contained a small silverside (Atherinidae) in its stomach. Because rotenone was not used it appears likely that the silverside was a normal dietary item. This solitary trumpet fish has frequently been observed to swim slowly over open areas and near coral heads and rubble. It appears to glide about, seldom seeking

cover. Although it has never been seen to capture food, its structural features suggest that it captures small prey by a rapid dilation of its mouth, particularly prey secluded in shallow holes or interstices into which it could probe with its long, tubular snout.

Family Fistulariidae

Species: *Fistularia petimba* (cornet fish)
Number examined: Bikini, 9 specimens
Sex: Males and females
Standard length: 500-700 mm
Digestive tract: Snout, long, tubular, jaws at end, very short and with an extremely small mouth opening, but capable of being broadened or narrowed, teeth small; alimentary tract straight.

Food item	Percentage of fish containing the item
Fish	
Labrids	77
Pomacentrids	33
Unid. small fish	33
<i>A. t. triostegus</i>	11
Balistids	11

This cornet fish occurs rather commonly in schools swimming near the surface, and occasionally in mid-water or near the bottom, in the quiet waters of the lagoon reef and leeward sea reefs. Frequently the schools lie quite motionless. It is obvious from the food items found that they frequent the vicinity of coral heads as well as cruise over the reef flats, and that they are capable of taking small fishes which are larger than the mouth opening of dead specimens. Hence, the extension of its flute-like snout is very important. We cannot agree with Suyehiro (1942) that this species takes only minute, floating creatures by utilizing its snout as a pipette. Our specimens contained nothing but small fish, although it is certain that swimming crustaceans, etc., would be taken if available. One of us has seen the species taken on a large bass plug in Hawaii.

Family Atherinidae

Species: *Stenatherina temmincki* (silverside)
Number examined: Bikini, 8 specimens; 1 empty
Sex: Males and females
Standard length: 85 mm
Digestive tract: Mouth moderately large, teeth weak; stomach absent, intestine moderately short, one loose coil

Food item	Percentage of fish containing the item
Crustacea	
Shrimp larvae	57
Copepods	28
Stomatopod larvae	14
Foraminifera and sand	57
Gastropoda	
Unid. small species	14
Fish	
Unid. fragments	14

This species occurs in very large schools near the surface or in mid-water. Some have been observed feeding from the bottom in very shallow water. Thus, observations as well as an analysis of the food items ingested indicate that this silverside feeds both on planktonic and benthonic forms.

Species: *Allanetta ovalua* (silverside)
Number examined: Arno, 12 specimens; 3 empty
Sex: Males and females
Standard length: 66-74 mm
Digestive tract: Similar to *S. temmincki*

Food item	Percentage of fish containing the item
Crustacea	
Calanoid copepods	88
Crab zoeae	44
Gastropoda	
Veliger larvae	11

This species swims near the surface and in mid-water in very large schools on all reefs visited. It behaves primarily as a selective feeder on zooplankton.

Species: *Pranesus pinguis* (silverside)
Number examined: Arno, 5 specimens: 3 empty
Sex: Males and females
Standard length: 66-74 mm
Digestive tract: Similar to *S. temmincki*

Both specimens containing food items had copepods and crab zoeae. This species has habits similar to *A. ovalana*, and is often found schooling with that species.

Family Summary

Atherinids are ubiquitous in large schools on virtually all reefs visited. For the most part they subsist on zooplankton, being rather selective in that they take mostly crustaceans and larval gastropods. At least one species, *S. temmincki*, feeds on the benthonic types of minute organisms when the school moves into very shallow, protected areas of the reefs.

Family Mugilidae

Species: *Neomyxus chavali* (mullet)
Number examined: Bikini, 3 specimens
Sex: Males and females
Standard length: 160-190 mm
Digestive tract: Teeth trifid setiform; stomach heavy-walled, but not gizzard-like; intestine very long, coiled

The three specimens examined all contained diatoms, desmids, and fine filamentous algae, some foraminiferans and detritus. This species apparently strains sandy bottom material from which it gets the minute algal forms and, perhaps only by inadvertence, picks up some minute animal species from the surface of the substrate.

Species: *Crenimugil crenilabis* (mullet)
Number examined: Arno, 11; Eniwetok, 2 specimens
Sex: Females and undeveloped
Standard length: 112-400 mm

Digestive tract: Stomach heavy-walled and a gizzard, but less heavy and with a greater lumen than in *Mugil cephalus*; intestine very long, coiled

Food item	Percentage of fish containing the item
Detritus and sand (fine)	92
Algae	
<i>Oscillatoria</i> sp.	84
Diatoms (<i>Nitzschia</i> sp. mostly)	61
Fine filamentous algae (appears scraped from compacted sandy bottoms)	15
Foraminifera	76

This species feeds quite similarly to the well known gray mullet, *Mugil cephalus*, except that larger items pass into the gut of *C. crenilabis*. It is frequently solitary or forms small schools in the less turbulent waters of the lagoon and seaward reefs. It is often seen feeding in very shallow water on compacted sandy or muddy bottoms.

Family Summary

Probably as much has been written about the digestive tract and food habits of the mullet as for any other group of fishes. The peculiar digestive tract of *Mugil cephalus* has been reported on in detail by many writers, since Cuvier and Valenciennes described it in the early nineteenth century. More recently Ghazzawi (1933, 1935) studied both morphological and histological features as well as the feeding habits of *M. cephalus* and *M. capito* in Egypt, and Al-Hussaini (1947) reported on a similar study for *M. auratus*; Suyehiro (1942) did likewise for *M. cephalus* in Japan; and

Hiatt (1947a) described feeding habits and alimentary tract morphology for *M. cephalus* in Hawaii. All agree that mullets feed predominantly on unicellular algae composing the benthos. Inadvertently, perhaps, they also ingest a considerable amount of the microfauna associated with the same habitat. The exceptionally long intestine and the triturating gizzard containing fine sand as an abrasive are evidence of mullets' primary dependence upon such forms as diatoms and desmids.

Family Sphyraenidae

Species: *Sphyraena genie* (barracuda)
Number examined: Eniwetok, 2 specimens: both empty
Sex: Female
Standard length: 1,220-1,240 mm
Digestive tract: Mouth large, pointed; large canine teeth; intestine short, straight

Both specimens examined were caught by hook and line near the garbage dump, and had no natural food items in their stomachs. Although this species is uncommon in the Marshall Islands it has been observed several times drifting solitarily near the surface stalking its prey. It surprises its victim with a sudden lunge. Barracuda probably also feed at mid-depth or near the bottom. Its main food is undoubtedly fish.

Family Polynemidae

Species: *Polydactylus sexfilis* (threadfin)
Number examined: Arno, 18 specimens: 12 empty
Sex: Undeveloped
Standard length: 57-86 mm
Digestive tract: Moderately short intestine

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	50
Crab fragments	33
Polychaeta	16
Foraminifera	
Calcarina sp.	16

Small specimens of this schooling species are found commonly on the reef shallows over sandy bottoms in protected areas. Larger fish are found along sandy beaches where the surf is rather strong. It feeds strictly on the benthonic fauna.

Family Scombridae

Species: *Gymnosarda nuda* (dogtooth tuna)
Number examined: Eniwetok, 2 specimens: both empty
Sex: Unknown
Standard length: 44-45 inches
Digestive tract: Several conical, pointed, canine-like teeth in jaws; stomach thick-walled; intestine short, almost straight

Neither of these specimens, caught by hook and line near a pass in the Eniwetok lagoon, had food in their stomachs, although others were often seen in small schools slashing through the dense schools of round herring near the pier. This species seems to swim more deeply than species of either *Katsuwonus* or *Euthynnus* which also occur inside the lagoons and in the surrounding seas. Dogtooth tuna are pelagic, rapid-swimming carnivores which grow to a large size. Woods (1953) mentions that this species had taken seads (*Decapterus muroadsi*) in the northern Marshalls, and the senior author noted the stomachs of this species at Bikini to contain seads (*Decapterus sanctaelenae*) as well as pelagic squid, flying fishes, and other small schooling types (Hiatt & Brock 1948).

Species: *Euthynnus affinis yaito* (little tunny)
Number examined: Observations only

No specimens of this species were available for food analysis, but small schools were observed repeatedly at

Eniwetok to slash through the dense schools of round herrings swimming near the pier. It is a rapid swimming, schooling, pelagic carnivore which feeds most often near the surface. It is known to take small fish, pelagic crustaceans, and pelagic squid (Welch 1950). The senior author has observed this species feeding among a dense school of atherinids at Arno which had surrounded him while skin-diving near the outer slope of the lagoon reef. The tunnys showed no concern whatever for the swimmer while slashing with great speed through the silversides, frequently as close as 5-6 ft from him. In another instance three medium-sized tunnys were observed herding a large school of several hundred scads, *Decapterus sanctachelena*, over a large coral knoll for over three hours in Rongerik Atoll in the northern Marshall Islands (Hiatt & Brock 1948). One lagging scad was captured by one of the tunnys. The entire performance was extraordinary, but probably typical, as Kishinouye (1923) also reports, although he singles this species out among the bonitos as the one which does not engage in herding prey.

Species: *Katsuwonus pelamis* (oceanic skipjack)

Number examined: Observations only

As with the other tunas reported herein, this schooling species was observed to slash repeatedly through the dense school of round herrings around the pier at Eniwetok. Because of its great economic importance and wide range the food and feeding habits of this species have been studied intensively. In Hawaii, Welch (1950) reports that this species subsists mainly on cephalopods, stomatopod larvae, and small fish, while Suyehiro (1942) and others in Japan have found this genus to feed principally on small or juvenile fishes, cuttle-fish, shrimps, schizopods, and amphipods.

Family Summary

The tunas are large, pelagic, fast-swimming, schooling carnivores which take virtually any prey of the proper size. Because of their pelagic nature, the food of those caught at sea consists mainly of schooling fishes, crustaceans, and squid which they capture by visual means. Those taken in lagoons or close to land appear to contain larval fishes and crustaceans which are produced by reef-and shore-dwelling adults. This type of food, supplementing the usual high seas forage species, probably is significant in attracting tunas close to mid-ocean islands.

Family Carangidae

Species: *Trachurus crumenophthalmus* (scad)

Number examined: Arno, 23; Bikini, 1; Eniwetok, 3 specimens: 4 empty

Sex: Males and females

Standard length: 85-245 mm

Digestive tract: Mouth moderately large, teeth small; stomach rather thick-walled; intestine rather short, with one loop

Food item	Percentage of fish containing the item
Foraminifera	
<i>Calcarina</i> sp.	47
<i>Marginopora</i> sp.	13
Gastropoda	
<i>Cerithium</i> sp.	26
Unid. small gastropods	17
Fish	
Unid. fragments	17
Crustacea	
Pelagic shrimps	8
Miscellaneous items	
Sand grains	30
Pebbles	26
Gurry	21

All specimens containing food were juvenile fish taken at Arno Atoll where they formed large schools which frequented the protected lagoon reef and inter-island reefs. Unlike most carangids (and this is perhaps an age characteristic) these scads fed principally on the benthonic fauna of the reef shallows, particularly the forms occurring on compacted sand. In all cases the foraminiferans eaten were enveloped in a viscous fluid which was probably associated with the digestive process. The adults of a closely related species in Japan, *Decapterus muroadsi*, were found by Suyehiro (1942) to have taken mostly larval fishes.

Species: *Trachinotus bailloni* (pompano)

Number examined: Arno, 9 specimens: 4 empty

Sex: Undeveloped

Standard length: 56-101 mm

Digestive tract: Mouth small; stomach thick-walled; intestine moderately short

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	100
<i>T. bailloni</i> , juveniles	20
Crustaceas	
Isopods	20
Crab fragments	20

This species is a slow-cruising carnivore which occurs in pairs or small schools. It lives rather close to shore in the lagoon shallows. The specimens examined were all juveniles, so the food of the adult of this pompano is unknown, but fish probably predominate in their diet as they do with the juveniles.

Species: *Carangooides ferdau jordani* (jack)

Number examined: Arno, 2; Eniwetok, 3 specimens: 2 empty

Sex: Males and females

Standard length: 250-395 mm

Digestive tract: Intestine short, straight

The three specimens containing food had eaten the following fish: *Bathygobius f. fuscus*, *Parupeneus trifasciatus*, unidentified goby, and unidentified fish fragments. This species grows rather large, and is a fast-swimming, roving carnivore on all reefs visited. It sometimes is seen schooling with other types of fish.

Species: *Caranx melanopterus* (jack)

Number examined: Arno, 1; Eniwetok, 1 specimen

Sex: Females

Standard length: 555 mm

Digestive tract: Intestine very short, straight

One specimen contained a small scad, *Trachurus crumenophthalmus*, and the other an unidentified fish fragment. This species, like *Carangooides ferdau jordani*, is a large, rapid-swimming, roving carnivore which prefers reef areas with considerable open water, either in lagoons, or in surge channels of the seaward reefs. It apparently feeds in mid-water close to coral mounds where it catches small coral-dwelling fish. In the Gilbert Islands Randall (1955) found the species to take coral-dwelling fish such as small wrasses.

Species: *Caranx lessoni* (jack)

Number examined: Eniwetok, 1 specimen: empty

Sex: Female

Standard length: 640 mm

Digestive tract: Intestine very short, straight

The single specimen was empty, but its observed habits are very much like *C. melanopterus*.

Species: *Elagatis bipinnulatus* (rainbow runner)

Number examined: Eniwetok, 2 specimens: 1 empty

Sex: Male and female

Standard length: 535-590 mm

Digestive tract: Mouth comparatively small, teeth in villiform bands; intestine short

The one specimen containing food in its stomach had a pelagic shrimp, a crab megalops, and some unidentified fish fragments. This species is a fast-swimming carnivore which is more or less pelagic. It is abundant around the pier at Eniwetok where it may be chummed to the surface easily. At intervals small schools of 5-10 individuals slash through the dense school of round herring near the pier. Its usual food is probably pelagic fish although it certainly will take swimming crustaceans or squid.

Family Summary

Many differences in feeding methods and predilections for food items occur among the several genera in this family, although all are carnivores. The smaller species, e.g., seads, frequently forage for benthonic fauna in very shallow water, although adult seads are seen most often in large schools in mid-water where they doubtless take small fish and pelagic invertebrates. The larger carangids, e.g., *Trachinotus*, *Carangoides*, and *Caranx*, feed mostly as roving carnivores, with *Trachinotus* inhabiting the more open water in small schools, and the other two genera inhabiting reef shallows and channels, mostly in a solitary fashion, where they feed upon small fish associated with the coral heads. They typically inhabit the deeper water just off the seaward reef edge during low tides, and move up onto the reef proper when the tide rises. *Elegatis bipinnulatus* is more pelagic than the other species and occupies a mid-water or surface position, usually in small schools. The small mouth suggests that only very small pelagic fishes and swimming crustaceans serve them as food.

Although no specimens were collected for examination, three separate observations of the jack, *Gnathanodon speciosus*, two at Arno, and one at Eniwetok are worthy of reporting. At Arno two fish of this species were observed swimming along-side the head of a large white-tipped shark, *Triaenodon obesus*, near the outer edge of the lagoon reef, at Eniwetok one fish was seen hovering about the head of a large nurse shark, *Ginglymostoma ferrugineum*, and three were observed at very close range swimming about the head of a giant sea bass, *Promicrops lanceolatus*. In no case were the sharks or the bass following the brilliantly yellow and black barred carangid, but the latter remained close to the head of the larger fish at all times.

The larger carangids are certainly one of the most important of the roving carnivores over all Marshallese reefs.

Family Apogonidae

Species: *Apogon novemfasciatus* (cardinal fish)
Number examined: Arno, 21; Bikini, 3 specimens: 7 empty
Sex: Males and females
Standard length: 34-70 mm
Digestive tract: Mouth large, small villiform teeth; stomach large, Y-shaped; intestine moderately short with one loop

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	35
Damsel fish	11
Wrasses	11
Unid. gobies	11
<i>Bathygobius f. fuscus</i>	5
<i>Amphiprion melanopus</i>	5
<i>Apogon frenatus</i>	5
Fish eggs	11
Crustacea	
Shrimp fragments	17
Xanthid crab fragments	17

This species is perhaps the most ubiquitous cardinal fish in the Marshall Islands. It lives beneath ledges or in caverns in rather large coral heads, and often aggregates into loose schools of several individuals. It is a voracious carnivore taking fish and crustaceans closely associated with the same coral head. These apogonids have never been observed more than a few feet away from their hiding place.

Species: *Apogon snyderi* (cardinal fish)
Number examined: Arno, 6; Bikini, 4; Eniwetok, 11 specimens: 3 empty
Sex: Males and females
Standard length: 54-110 mm
Digestive tract: Similar to *A. novemfasciatus*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	38
Xanthid crabs	22
Ostracods	11
Copepods	5
<i>Alpheus</i> sp.	5
Isopods	5
Fish	
Unid. fragments	27
Gastropoda	
<i>Cerithium</i> sp.	5

This solitary species lives mostly around coral mounds on the lagoon reefs near the outer slope at depths of 10-15 ft; but some have been taken in protected ocean reef shallows. It dwells in crevices and caverns in the coral, and subsists mainly on small fish and crustaceans in the immediate vicinity of its hiding place. Randall (1955) found this species to have taken small fish and crustaceans in the Gilbert Islands.

Species: *Apogon exostigma* (cardinal fish)
Number examined: Arno, 5 specimens: 1 empty
Sex: Females
Standard length: 45-53 mm
Digestive tract: Similar to *A. novemfasciatus*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	50
Fish	
<i>Eviota</i> sp.	25
Polychaeta	25

Species: *Apogon nigrofasciatus* (cardinal fish)
Number examined: Eniwetok, 3 specimens
Sex: Female and undeveloped
Standard length: 52-68 mm
Digestive tract: Similar to *A. novemfasciatus*

Two of the specimens examined contained unidentified shrimps; one contained, in addition, and unidentified polychaete. The remaining specimen contained an alpheid shrimp. This species is common on both the seaward reef shallows and on the lagoon reefs, living under ledges and in interstices of coral mounds. Its food consists of items closely associated with the same coral heads.

Species: *Apogon noraequinæ* (cardinal fish)
Number examined: Eniwetok, 2 specimens
Sex: Undeveloped
Standard length: 36-41 mm
Digestive tract: Similar to *A. novemfasciatus*

Both specimens examined had taken shrimp, and one had, in addition, the abundant foraminiferan, *Calcarina* sp. This species, common both on seaward and lagoon reefs, in crevices and holes in coral mounds, is sometimes found in close association with echinoids. The foraminiferan in one specimen suggests that at times it feeds on benthonic fauna.

Species: *Apogon erythrinus* (cardinal fish)

Number examined: Eniwetok, 1 specimen

Sex: Female

Standard length: 34 mm

Digestive tract: Similar to *A. novemfasciatus*

This specimen contained unidentified fish fragments and an unidentified polychaete. This species is common about crevices and caves in coral mounds on both seaward and lagoon reefs down to depths of at least 18 feet.

Species: *Apogon* sp. (cardinal fish)

Number examined: Bikini, 3 specimens

Sex: Males and females

Standard length: 85-90 mm

Digestive tract: Similar to *A. novemfasciatus*

All specimens contained remains of shrimps, one an alpheid shrimp, another a *Leander* sp., and the third had unidentified shrimp fragments.

Species: *Gymnapogon philippinus* (cardinal fish)

Number examined: Arno, 3 specimens: 2 empty

Sex: Females

Standard length: 35-40 mm

Digestive tract: Mouth large, teeth erect, large canine teeth on vomer; intestine short

The single fish with food items in its stomach contained fish eggs. We cannot be certain that these are not eggs of this species which may have been "incubating" in the mouth of the fish, as some of the cardinal fish are known to do. Its large canines suggest that it is a voracious carnivore. This species lives beneath ledges and in interstices of living or dead coral heads, particularly on the protected seaward reefs. It has never been seen alive by the authors, despite many hours of intensive observation in its habitat. Thus, it is probably very secretive during the day and forages at night. The empty stomachs add evidence to this suggestion.

Species: *Paramia quinquefasciata* (cardinal fish)

Number examined: Arno, 8 specimens

Sex: Males and females

Standard length: 36-55 mm

Digestive tract: Mouth large, canines weak; intestine short

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	37
<i>Eriota</i> sp.	12
Wrasses	12
Crustacea	
Shrimp fragments	25
Crab fragments	12
Gastropoda	
<i>Atys</i> sp.	12

This species is very shy, seldom seen, and lives under ledges and in caves, rarely in interstices of coral heads. It apparently forages on the benthonic fauna of sandy areas adjacent to its hiding place, as the eleotrid, *Eriota* sp., and the gastropod, *Atys* sp., are benthonic, sandy-substrate dwellers.

Species: *Cheilodipterus macrodon* (cardinal fish)

Number examined: Bikini, 1 specimen

Sex: Male

Standard length: 90 mm

Digestive tract: Mouth large, numerous fang-like canines in jaws; intestine short.

The single specimen examined had eaten a blenny, *Istiblennius* sp. This species was common in the deeper reef areas of the lagoon at Bikini, but uncommon or rare in a similar habitat at Eniwetok. It is solitary and lives under ledges near mounds of rubble or living coral. This species is one of the largest apogonids in the Marshall Islands.

Family Summary

The cardinal fishes all have rather similar habits, although the dental armature varies appreciably among the several genera found in the Marshall Islands. All are voracious carnivores, taking fish, crustaceans, and other invertebrates if they are of the proper size. Suyehiro (1942) reports that *Apogon lineatus* and *A. semilineatus* of Japan take small crustacean and larval fish. Suyehiro also points out an interesting situation, with which our observations also agree, that when the ovaries are well developed the females cease to take food. We found this to be the case with every species in which the females had eggs nearing maturity. Most species apparently forage diurnally, although at least one species appears to be a nocturnal feeder.

Ordinarily cardinal fishes occur solitarily, or in rather small schools, although some species not covered in this study form dense schools over and in patches of certain living, branching corals, and others form large schools confined to coral mounds with large caverns in which they hide if disturbed. *A. novaeguineae* has been observed to swim among the long spines of diadematid sea urchins, particularly *Echinothrix diadema*, when both the urchin and fish are secluded in crevices or holes in coral mounds. When the urchin is moved outside the hole a short distance some of the cardinal fish venture out and take station among the spines. However, they will not do this if the urchin is moved too far away from the hole or crevice.

Several specimens were found with fish eggs in their stomachs. The presence of these could have resulted from the accidental convulsive swallowing of "incubating" eggs held in the mouth during rotenone poisoning.

Family Priacanthidae

Species: *Priacanthus cruentatus* (big-eye)

Number examined: Eniwetok, 13 specimens

Sex: Males and females

Standard length: 100-235 mm

Digestive tract: Teeth villiform, short; intestine short

Food item	Percentage of fish containing the item
Cephalopoda	
<i>Octopus</i> sp.	84
Crustacea	
Pelagic shrimps	53
Shrimp fragments	15
Alpheid shrimps	7
Stomatopod fragments	53
Xanthid crab fragments	15
Portunid crab	7
Crab megalopa	7
Isopods	7
Fish	
Unid. fragments	46
Polychaeta	
Unid. polychaetes	23

This species is locally abundant, particularly on lagoon reefs where there are large crevices or caverns in living coral or coral rubble. Because of its especially large eyes and spelean habitat, most marine biologists have considered this genus to comprise nocturnal feeders. However, the bulk of the food taken by the specimens examined were octopi (*Octopus* sp.) and many had retained the beaks of previously digested ones in their stomachs. It is therefore conceivable that the cryptic habits of both octopi and big-eyes combine to provide these fish a source of food during the daytime. The fact that no stomachs of this species were empty, yet many stomachs of the associated holocentrids (squirrel fish) were empty, leads us to suspect that the big-eye is an active day feeder, but may also forage at night.

Both swimming and bottom-dwelling organisms are taken in amounts which indicate that this species is not restricted in its foraging habits to any particular locality on the reef, but rather is an opportunist. The polychaetes found so abundantly in a few stomachs were a type common in the sandy bottoms adjacent to coral and rubble mounds. Members of this family are abundant carnivores, feeding in caverns, in mid-water and on coral mounds and sandy bottoms.

Family Serranidae

Species: *Epinephelus merra* complex (grouper)
Number examined: Arno, 25; Bikini, 6 specimens: 6 empty
Sex: Males and females
Standard length: 99-360 mm
Digestive tract: Mouth large, outer teeth on jaws villiform, inner rows larger and depressible, short canines at symphyseis of each jaw; stomach large, heavy-walled; intestine medium length with a long loop

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	28
<i>Gymnothorax marginatus</i>	4
<i>Allanetta ovalis</i>	4
<i>Parupeneus trifasciatus</i>	4
<i>Holocentrus sammara</i>	4
Holocentrid fragments	4
Unid. goby	4
Larval fish	4
Unid. small fish	8
Crustacea	
Crab fragments	24
Portunid fragments	8
<i>Petrolisthes</i> sp.	4
Hippolytid shrimp	4
Shrimp fragments	4
Stomatopod fragments	8
<i>Galathea</i> sp.	4

Essentially, four species are grouped together here which were not segregated taxonomically until after our food analyses had been made and the specimens thrown away. The species involved are *merra*, *hexagonatus*, *spilotus*, and *elongatus*. All four have similar appearance and behavior, and occupy essentially the same habitat.

These species are very abundant, demersal, small carnivores which live under ledges near the bottom of coral mounds and rubble. Frequently, they are seen lying motionless on the surface of massive coral formations. They occurred on all reef shallows visited. These groupers forage by lying in wait for prey species to move sufficiently close to them at which time they dash out and seize the victim in their large mouths. No particular selection is made among prey species; they take any small fish or crustaceans which happen by.

Species: *Epinephelus fuscoguttatus* (grouper)
Number examined: Arno, 4; Eniwetok, 4 specimens: 3 empty
Sex: Females
Standard length: 240-360 mm
Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Fish	
<i>Holocentrus diadema</i>	20
<i>Parupeneus trifasciatus</i>	20
<i>Spratelloides delicatulus</i>	20
Unid. fragments	20
Crustacea	
<i>Thalamita</i> sp.	20
Shrimp fragments	20
Gurny	20

This large solitary grouper is commonly observed lying motionless on the bottom, frequently some distance from protective cover. It also commonly hides under large corals such as *Acropora reticulata* and under rock ledges. This species is one of the commonest large carni-

vores found on all reefs where the water is six or more feet in depth.

Species: *Epinephelus kohleri* (grouper)
Number examined: Arno, 1; Eniwetok, 1 specimen: 1 empty
Sex: Males
Standard length: 325-370 mm
Digestive tract: Similar to *E. merra*

The one specimen with food contained fish fragments. This species is a large, strongly demersal grouper which usually lies on the bottom near the base of a coral mound in water from 6 to 30 feet in depth. It does not stay away from its refuge place as does *E. fuscoguttatus*. At no place was this species common.

Species: *Epinephelus hexagonatus* (grouper)
Number examined: Bikini, 6 specimens: 2 empty
Sex: Males and females
Standard length: 105-290 mm
Digestive tract: Similar to *E. merra*

Each of the four specimens had taken different species of food items although three of them contained only fish, *Pempheris ovalensis*, a juvenile trigger fish, and *Pseudochelidinus* sp. The other specimen had many polychaete fragments in its stomach. This species has the same habits and is found in the same localities on the reefs as is *E. merra*, described earlier.

Species: *Epinephelus macropsilus* (grouper)
Number examined: Eniwetok, 2 specimens: 1 empty
Sex: Female
Standard length: 240-290 mm
Digestive tract: Similar to *E. merra*

The specimen containing food had only fragments of polychaetes. This species, uncommon on most reef areas, grows to about one foot in length, and lurks under expansive coral heads and rock ledges, seldom venturing far from protective cover. Although the specimen examined contained only polychaetes, it is reasonable to expect this species to have food habits similar to other groupers and to take fish, crustaceans, and other invertebrates on occasion.

Species: *Epinephelus spilotus* (grouper)
Number examined: Eniwetok, 12 specimens: 4 empty
Sex: Males and females
Standard length: 170-315 mm
Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Fish	75
Crustacea	
Crab fragments	25
Shrimp fragments	12
<i>Stenopus hispidus</i>	12
Cephalopoda	
<i>Octopus</i> beaks	12
Sand and pebbles	37

This was a common grouper on all reefs visited. It appears sluggish, often hiding in coral heads or under ledges, but sometimes is seen lying motionless on the bottom well away from protective cover. Its food and feeding habits are similar to other groupers of similar size.

Species: *Variola louti* (grouper)
Number examined: Bikini, 2 specimens: 1 empty
Sex: Female
Standard length: 400 mm
Digestive tract: Similar to *E. merra*

The one specimen with food in its stomach had taken a juvenile surgeon fish, *Naso* sp. This species was uncommon on most reefs visited, preferring lagoon reefs to seaward ones, and was found in deeper water than most

other groupers, usually depths in excess of 10 ft. It is solitary, and lives around the deeper coral heads, but frequently is seen hovering in mid-water. It attains a length of about 3 ft, and seems much more agile than other groupers.

Species: *Cephalopholis urodelus* (grouper)

Number examined: Eniwetok, 17; Arno, 3 specimens: 7 empty

Sex: Females and undeveloped

Standard length: 65-190 mm

Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	42
Crustacea	
Alpheid shrimp fragments	28
Xanthid crab fragments	14
Porcellanid crab fragments	7
Sand grains	7

This species attains about one foot in length, and lurks in holes and crevices of coral heads in all reef areas at depths of 10-12 ft. It is strongly demersal and seldom ventures more than a few feet from its place of refuge.

Species: *Cephalopholis miniatus* (grouper)

Number examined: Eniwetok, 1 specimen: empty

Sex: Undeveloped

Standard length: 280 mm

Digestive tract: Similar to *E. merra*

This is a large, demersal carnivore which lives at considerable depths in the lagoons. It was never observed on the reefs, but several individuals frequented the garbage dump at Eniwetok. Its structure and habits indicate that it is predaceous and probably feeds, like other large groupers, mostly on fish and crustaceans.

Species: *Cephalopholis argus* (grouper)

Number examined: Arno, 3; Bikini, 1; Eniwetok, 8 specimens: 3 empty

Sex: Males and females

Standard length: 130-430 mm

Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	33
Unid. fragments	11
Fish	
Abudedefduf dickeni	11
Mullid fragments	11
Unid. fragments	22
Polychaeta	
Unid. polychaetes	11

This medium-sized grouper is common around coral heads from depths of 3-30 ft or more on most reefs. It is a rather active, demersal species which lies in wait for its prey beneath ledges and coral heads. In the Gilbert Islands one specimen of this species examined had taken a shrimp (Randall 1955).

Species: *Anyperodon leucogrammicus* (grouper)

Number examined: Eniwetok, 5 specimens: 2 empty

Sex: Males and females

Standard length: 230-350 mm

Digestive tract: Similar to *E. merra*

One of the three specimens with food had unidentified fish fragments in its stomach; another had a goat fish and the third had only the foraminiferan, *Calcarina* sp., along with sand grains of the same size, caught in the folds of its stomach mucosa. This species is uncommon, but present in lagoon reef areas and seaward reefs where the water is not turbulent. It secludes itself under corals almost all of the time, and is rarely observed by the skin-diver. Doubtless it lies motionless under

corals watching for fish or invertebrates to pass by closely enough so that it may lunge out to seize them.

Species: *Plectropomus truncatus* (grouper)

Number examined: Eniwetok, 3 specimens: 2 empty

Sex: Undeveloped

Standard length: 295-600 mm

Digestive tract: Similar to *E. merra*, but with enlarged canines.

The one specimen containing food had a squirrel fish, *Holocentrus* sp., in its stomach. This species is common on reefs having an abundance of living coral from 4-20 ft in depth. It is more active and less demersal than other groupers, characteristically hovering in mid-water. It is shy and difficult for a swimmer to approach. It especially hovers in surge channels of the seaward reefs, or just over the reef front 6-20 ft below the surface. Although only one of the three specimens examined contained a fish as food, it is rather certain that fish are the principal food items taken.

Family Summary

Although all the members of this family are voracious carnivores ubiquitous on Marshallese coral reefs, there are great differences in habits between the smaller and larger species, and among the larger species certain pertinent differences occur. Most of the smaller species are demersal and conceal themselves in crevices or holes in corals, or under ledges and rocks in coral rubble. Their characteristic habit is to lie motionless on the bottom, mostly concealed by the coral except for the head always directed outward, where they lie in wait for unwary small fish or invertebrates to come within their reach. A rapid lunge of a few inches to a few feet is made to catch their prey. Some of the larger species can always be found lying motionless on sandy or rubble bottoms just a few feet from coral mounds. They appear to pay little attention to swimmers at the surface, but little by little they move further outward to deep water.

Certain of the larger species, notably *V. louti*, characteristically hover in mid-water near the coral caverns in which they seclude themselves. Still others, *Plectropomus truncatus* and *P. leopardus*, hover in mid-water over open areas in surge channels, just over the seaward reef edge, or near coral mounds and patches in deeper water on the lagoon reefs.

Groupers are not notoriously rapid swimmers; hence, even those larger forms which hover in open water, or those which are demersal and lie motionless on the bottom, probably subsist to a great extent on crustaceans and coral-dwelling fish which venture too closely to them. It is doubtful that they could catch other mid-water fishes.

Family Pseudochromidae

Species: *Plesiops melas*

Number examined: Arno, 15; Eniwetok, 1 specimen: 1 empty

Sex: Males and females

Standard length: 36-58 mm

Digestive tract: Mouth large, teeth in villiform bands on both jaws; intestine short.

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	33
Hermit crab fragments	13
Xanthid crab fragments	6
Shrimp fragments	6
Alpheus sp. fragments	6
Fish	
Unid. fragments	20
Eviota sp.	13
Gastropoda	
Unid. gastropod fragments	20
Sand	6

This species, common at Arno, was rather uncommon at Eniwetok. It lives on the interisland reef and seaward reefs where the wave action is rather strong. The species is demersal and hides in and under living coral. It characteristically remains motionless while lying in wait for its prey which comprises members of the benthonic fauna.

Species: *Plesiops nigricans*
Number examined: Arno, 6 specimens
Sex: Males and females
Standard length: 74-119 mm
Digestive tract: Similar to *P. melas*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	50
<i>Portunus longispinosus bidens</i>	17
Xanthid crab fragments	17
<i>Coenobita</i> sp.	17
Hermit crab fragments	17
<i>Galathea</i> sp.	17
Copepods	17
Fish	
Unid. fragments	34
<i>Abudefduf glaucus</i>	17
<i>Apogon novemfasciatus</i>	17

This species was especially common at Arno Atoll on the seaward reef shallows. It is mainly an intertidal species and is commonly found stranded in small tide pools containing loose boulders, or even under rocks completely exposed at low tide. It is a voracious carnivore which apparently darts out from its hiding place to seize its prey which consists of benthonic intertidal crustaceans and small fish associated with corals in shallow water, or tide pool inhabitants.

Species: *Pseudogramma polyacantha*
Number examined: Arno, 13; Bikini, 3 specimens: 5 empty
Sex: Males and females
Standard length: 28-65 mm
Digestive tract: Similar to *P. melas*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	54
Crab fragments	27
Xanthid crab fragments	9
Fish	
Unid. fragments	9

This species was uncommon at Eniwetok, but rather abundant at Arno Atoll, on both the lagoon and seaward reef shallows near living coral. It habitually hides in and under living coral and has a demersal nature. Like others of this family it lies in wait for prey to come sufficiently close to capture, and thus feeds mostly on benthonic crustaceans and small fish associated with living coral.

Species: *Pseudochromis tapeinosoma*
Number examined: Arno, 2 specimens
Sex: Males
Standard length: 29-37 mm
Digestive tract: As in *P. melas*, except that jaws contain teeth in villiform bands and strong canines

Both specimens examined had taken small crustaceans, and contained crab fragments, isopods, and copepods. This very small species, uncommon at Eniwetok, was common both at Bikini and at Arno in living coral both on the lagoon and seaward reefs. It is demersal, and doubtless feeds by lying in wait for small crustaceans to come close to it.

Family Summary

All species of this family live under ledges and rocks and in interstices of living corals, rather similar in

habits to the demersal groupers. Only *P. nigricans* is found in the intertidal zone where it is a characteristic carnivore in tide pools. All are voracious carnivores, although small in size, feeding predominantly on crustaceans, but taking any prey the proper size. Their characteristic feeding method is to lie in wait for prey species to come near enough for capture, which is then accomplished by a rapid lunge.

Family Pempheridae

Species: *Pempheris ovalensis* (sweeper)
Number examined: Bikini, 11; Eniwetok, 5 specimens: 1 empty
Sex: Males and females
Standard length: 75-180 mm
Digestive tract: Mouth moderate in size, teeth in villiform bands on the jaws; intestine short

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	26
Alpheid shrimps	6
Xanthid crab fragments	26
<i>Trapezia</i> sp.	20
Crab megalopa	20
Stomatopod fragments	13
<i>Odontodactylus</i> sp.	6
Copepods	6
Polychaeta	
Unid. pelagic polychaetes	20
Polynoid polychaetes	6
Cephalopoda	
<i>Octopus cyanea</i>	6
Fish	
Juvenile wrasses	6

Sweepers are abundant locally at all three atolls, most commonly in seaward reef surge channels or under overhanging reef ledges at the seaward edge where they are subjected to severe wave action. Frequently large numbers school at the head of surge channels. They also occur commonly on the lagoon reef around large coral mounds in water 10-20 ft in depth. They appear to be voracious carnivores usually having the stomachs crammed with food, mainly crustaceans.

Family Lutjanidae

Species: *Lutjanus monostigma* (snapper)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Female
Standard length: 345-365 mm
Digestive tract: Mouth large, canines well developed on sides of jaws; stomach thick-walled; intestine short, one loop

The single specimen containing food had eaten several goat fish (Mullidae). This species does not wander about, but remains in small schools in the deeper waters of the lagoon reef. Frequently, it may be seen in large caverns in the coral mounds. The young swim in larger schools on the seaward reef shallows and interisland reef shallows.

Species: *Lutjanus bohar* (snapper)
Number examined: Bikini, 2 specimens: 1 empty
Sex: Males
Standard length: 470-550 mm
Digestive tract: Similar to *L. monostigma*

The one specimen containing food had unidentified fish fragments in its stomach. This large snapper was never seen in the shallow reef areas, but was seen occasionally in deeper water down the lagoon reef slope or off the seaward reef edge. It is a hovering, mid-water carnivore.

Species: *Lutjanus vitta* (snapper)
Numbers examined: Arno, 2; Eniwetok, 24 specimens: 8 empty
Sex: Males and females
Standard length: 161-255 mm
Digestive tract: As in *L. monostigma*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	38
Portunid crabs	27
Crab fragments	27
Stomatopod fragments	5
Fish	
Unid. fragments	11
<i>Spratelloides delicatulus</i>	11
Polychaeta	
Unid. fragments	5
Chordata	
<i>Ptychoderma</i> sp.	5

This snapper is very abundant in the Marshall Islands, and was observed commonly in schools, comprised, frequently, of both *L. vittata* and *L. gibbus*, along rocky ledges bordering sandy patches. It was also observed frequently in large holes 6-8 ft deep in the interisland reefs at Eniwetok. Apparently, it feeds from the surface to the bottom, as the food items range from surface swimming round herring, *S. delicatulus*, to fossorial balanoglossids, *Ptychoderma* sp.

Species: *Lutjanus vaigiensis* (snapper)
Number examined: Arno, 6 specimens
Sex: Undeveloped
Standard length: 33-58 mm
Digestive tract: Similar to *L. monostigma*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	50
Amphipods	33
Shrimp fragments	17
Stomatopod fragments	17
Fish	
Unid. fragments	50

The specimens examined were all juveniles taken from a large school on the lagoon reef at Arno in water about 5 ft deep. At this age they apparently feed mostly on the benthonic fauna in shallow water. The adults reach about 18 inches in length, and probably have different habits than those indicated here for the juveniles. However, Randall (1955) reported on the food of two larger *vaigiensis* from the Gilbert Islands and listed a small crab for one and a small holothurian for the other, both benthonic forms.

Species: *Lutjanus gibbus* (snapper)
Number examined: Arno, 1; Eniwetok, 32 specimens: 10 empty
Sex: Males and females
Standard length: 175-260 mm
Digestive tract: Similar to *L. monostigma*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	60
Portunid crab fragments	17
<i>Kraussia rugulosa</i>	8
Parthenopid crabs	4
Hermit crabs (<i>Calcinus</i> sp.)	4
Alpheid shrimp	4
Alpheus ventrosus	4
Shrimp fragments	4
Amphineura	
Solenogastrid (<i>Neomenius</i> sp.)	13
Cephalopoda	
<i>Octopus</i> sp.	4
Gastropoda	
<i>Natica</i> sp.	4
Chordata	
<i>Ptychoderma</i> sp.	4
Echinodermata	
Small unid. holothurians	4
Polychaeta	
Unid. polychaetes	4
Sipunculidae	
Unid. fragments	4
Fish	
<i>Apogon erythrinus</i>	4

This snapper is one of the most abundant in the Marshall Islands. It is seen commonly on all reefs, particularly in the interisland reefs where coral growth is luxuriant and the water is at least 6-8 ft deep. At Arno huge schools moved back and forth just beyond the seaward reef edge. It feeds just about everywhere on the reefs, taking species commonly associated with living, branching corals, and benthonic fauna characteristic of sandy bottoms, some of which are fossorial species. It depends primarily upon crustaceans, the bulk of which are sandy-bottom dwellers.

Species: *Sclopsis cancellatus* (snapper)
Number examined: Arno, 3 specimens: 1 empty
Sex: Males and females
Standard length: 40-137 mm.
Digestive tract: Similar to *L. monostigma*

One specimen contained crab fragments and the other had only gurry. This species lives near branching corals, especially at the protected seaward reef edge and the lagoon reef edge. Because of its structure and habits it is probably predaceous on crustaceans and small fish.

Species: *Gymnocranius griseus* (snapper)
Number examined: Arno, 1; Eniwetok, 1 specimen
Sex: Female
Standard length: 298-375 mm
Digestive tract: Mouth moderate in size, teeth short, canines near symphyses of jaws, rounded and molariform on sides of jaws; stomach heavy-walled; intestine moderately short with slight looping

In the two specimens examined the following food items were found: Crustacea—*Thalamita* sp., Xanthid crab fragments; Echinodermata—*Holothuria* sp. (entire specimen), *Mareta* sp. (heart urchin); Pelecypoda—Unid. clam.

This species has rather different food habits than other lutjanids examined, as would be expected from its highly modified dentition. It is strictly a feeder on the benthonic fauna, and more particularly on the fossorial types, many of which are hard shelled and must be crushed before being digested. It has been observed in the process of foraging on sandy bottoms where it "blows" the sand away from buried prey. *G. griseus* is a rather slow-swimming "solemn" appearing fish. It is often seen in groups of two or three individuals hovering around large coral mounds adjacent to open sandy areas. They slowly circle these coral mounds keeping an eye on skin divers.

Species: *Lethrinus microdon* (snapper)
Number examined: Eniwetok, 2 specimens
Sex: Male and female
Standard length: 270-340 mm
Digestive tract: Similar to *L. monostigma*

The two specimens examined had eaten the following: Crustacea—Maiid crab; Portunid crab; Crab fragments; Fish—Unid. fragments.

This species is solitary and occurs only in the deeper water over the lagoon reef slope. None were seen in water shallower than 15 ft. According to the food items eaten, the species must swim close to the bottom where it feeds on benthonic crustaceans primarily. Al-Hussaini (1947) reports that two species of this genus in the Red Sea also prefer benthonic crustaceans, but take a wide variety of prey, including echinoderms and molluscs.

Species: *Apion virescens* (streaker)
Number examined: Eniwetok, 3 specimens: all empty
Sex: Males and females

Standard length: 540-760 mm
Digestive tract: Mouth very large, teeth strongly developed, heavy canines; intestine moderately short

The specimens examined had been eating garbage, but this species is a large, solitary, voracious carnivore which hovers in mid-water over the lagoon reef slope from 10-40 ft in depth. It will cruise quite slowly up to the shallows in search of prey, but when disturbed it moves back into deeper water, where it swims along the bottom. At no time have we seen this fish feeding, except during rotenone poisoning stations, but there is no doubt about its niche being that of a voracious, roving carnivore on the lagoon reefs.

Species: *Gnathodentex aureolineatus*
Number examined: Bikini, 4 specimens
Sex: Males and females
Standard length: 160-180 mm
Digestive tract: Both jaws with outer row of conical canines, three pairs of which are enlarged at front of jaws; intestine moderately short

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crabs	100
Gastropoda	
<i>Cerithium</i> sp.	75
Polychaeta	
Unnid. fragments	25
Fish	
<i>Stenatherina temmincki</i>	25
Unnid. fragments	25

This species frequents the relatively deep water over the lagoon reefs and the surge channels along the seaward reef margin. It is apparently a solitary carnivore which takes both food at the surface or in mid-water (silversides) and benthonic fauna (xanthid crabs, polychaetes and gastropods).

Family Summary

Snappers are all carnivorous fish, with one possible exception, *Macolor niger*, which will be discussed below. They vary in size from small fish a few inches in length to some of the largest of the reef-dwelling species, exceeding 3 ft. Several species school (*Lutjanus ka mura*, *gilbus*, *vitta*), but most are solitary or occur as loosely organized aggregations. The largest species, i.e., *L. bohar*, and *A. virescens*, are solitary. All have large mouths and strong dentition. By and large they seem to be predominantly benthonic feeders and swim just above the bottom. A few, of which *A. virescens* is a good example, are mid-water forms. At least three species, *L. vitta*, *L. gibbus*, and *Gymnocranius griseus*, take fossorial forms, with the latter species having developed the proper dentition and habits to feed almost exclusively on hard shelled clams, heart urchins, and gastropods. Except for *G. griseus* very little specificity is shown in types of prey taken; most capture any type of fish or invertebrate which they contact and can handle. Randall (1955) examined a few lutjanids in the Gilbert Islands and found similar feeding habits to those described here.

One species, *Macolor niger*, was taken by hook and line from the Eniwetok pier, so was not included in the food study. However, its great divergence in food habits and structural features from the usual snapper make it worthwhile to mention here. This species has the gill rakers modified for sieving plankton and they project well forward into the buccal cavity. However, the fact that it was caught on a baited hook indicates that it is by no means restricted to a planktonic diet. Species of the genus *Caesio* are full-fledged plankton

feeders, but none were collected for our study. Randall (1955) reports the food of *C. xanthonotus* in the Gilbert Islands to consist of pelagic copepods, mollusc larvae, shrimp nauplii, and fish eggs.

Thus, the family Lutjanidae comprises a heterogeneous group of fishes as regards their food and feeding habits and associated structural modifications. This heterogeneity is reflected in the many taxonomic changes made by successive authors in evaluating the parameters of this family.

Family Leiognathidae

Species: *Gerres argyreus* (silver perch)
Number examined: Arno, 2 specimens
Sex: Female
Standard length: 133-186 mm
Digestive tract: Rather long, highly protrusible snout, small teeth in villiform bands on both jaws; stomach thin-walled; intestine long, coiled.

The following food items were found in the two specimens examined: Crustacea—Isopods, Ostracods; Polychaeta—Unid. polychaetes; Foraminifera; Algae—Algal scrapings, little sand; Algal filaments, little sand.

Silver perch are solitary individuals distributed usually over sandy bottoms in quiet lagoon reef waters from 6-30 ft. deep. They work busily at stirring up the surface layers of the bottom with their protrusible snouts, taking anything edible. They are clearly omnivorous in habits, a fact reflected by the long, coiled intestine and thin-walled stomach. Al-Hussaini (1947) found *G. oyena* in the Red Sea to prefer polychaetes, but to take also such items as small crustaceans, fish, and other organisms.

Family Sparidae

Species: *Monotaxis grandoculis*
Number examined: Arno, 3; Eniwetok, 5 specimens: 1 empty
Sex: Males and females
Standard length: 195-250 mm
Digestive tract: Mouth moderately large, both jaws with a single row of molar teeth, the posterior few very broad and heavy, strong canines at front of both jaws; stomach heavy-walled; intestine of medium length.

Food item	Percentage of fish containing the item
Gastropoda	
Crushed <i>Alys</i> sp. and <i>Cerithium</i> sp.	100
Pelecypoda	
Crushed sand-dwelling clams, few whole	71
Crustacea	
Crushed crab fragments	42
Portunid crabs	28
Parthenopid crabs	14
Hermit crabs (crushed gastropod shells)	28
Echinodermata	
Small spatangids, crushed	14
Polychaeta	
Unnid. polychaetes	14

This species is always found alongside coral mounds, swimming slowly or hovering over sandy patches. It is most often solitary, but does form loose aggregations of two or three individuals at times. Its food habits and dental structure designate it as a feeder on fossorial forms, taking hard-bodied species which are crushed with the massive grinding-, crushing-type molariform teeth. When feeding this fish virtually stands on its head and "blows" away the sand surrounding its prey. Randall (1955) found specimens in the Gilbert Islands to feed as reported here.

This genus is frequently included with the family Lutjanidae (Schultz et al. 1953). However, we believe that it is sufficiently distinct, structurally and behavioristically, to merit its taxonomic segregation.

Family Mullidae

Species: *Mullidichthys samoensis* (goatfish)
Number examined: Arno, 19; Bikini, 7; Eniwetok, 8 specimens:
11 empty

Sex: Males and females

Standard length: 81-250 mm

Digestive tract: Chin with barbels, mouth medium, teeth minute;
stomach V-shaped; intestine medium-long

Food item	Percentage of fish containing the item
Fish	
Gurny	42
Unid. fragments	28
Polychaeta	
Unid. polychaetes	14
Sabellids	4
Crustacea	
Shrimp fragments	14
Crab fragments	9
Hermit crab fragments	9
Cyclopoid copepods	9
Pelecypoda	
<i>Semelangulus</i> sp.	14
Gastropoda	
Crushed gastropods	9
Echinodermata	
Spatangid fragments	9
Chordata	
<i>Ptychoderia</i> sp.	4
Sand, including foraminiferans	14

This species was found in large schools of 25-100 individuals swimming over and probing sandy bottoms with their barbels. They are especially abundant on shallow lagoon shores and on seaward reef flats when the tide is high. As its food items indicate, it consumes flesorial as well as surface benthonic fauna. At Eniwetok the specimens examined had been feeding heavily on the small clam, *Semelangulus* sp.

Species: *Parupeneus trifasciatus* (goatfish)

Number examined: Arno, 27 specimens: 3 empty

Sex: Males and undeveloped

Standard length: 46-150 mm

Digestive tract: Similar to *M. samoensis*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	17
Maillid crab fragments	12
Shrimp fragments	33
Unid. shrimps	17
<i>Alyhev's</i> sp.	17
Cyclopoid copepods	12
Calanoid copepods	8
Copepod metanauplii	4
Ostracods	8
Tanaid isopods	8
Amphipods	4
<i>Galathea</i> sp.	4
Fish	
Unid. fragments	20
Gastropods	
<i>Olivia</i> sp.	12
Polychaeta	
Unid. polychaetes	4
Foraminifera	
<i>Calcarina</i> sp.	8

P. trifasciatus is a small goatfish which occurs in groups of two or three on virtually all reefs from 3-10 ft deep. Frequently it is seen probing the sand with its barbels around the base of coral heads. It forages in typical goatfish fashion, but takes mostly smaller crustaceans, other invertebrates, and small benthonic fish. In the Gilbert Islands, Randall (1955) reported this fish to have consumed amphipods, copepods, and other small crustaceans.

Species: *Parupeneus barberinus* (goatfish)

Number examined: Arno, 9; Eniwetok, 3 specimens

Sex: Males

Standard length: 60-390 mm

Digestive tract: Similar to *M. samoensis*

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	58
Crustacea	
Shrimp fragments	41
Ostracods	25
Isopods	25
<i>Thalamita</i> sp.	17
<i>Tetralia globerrima</i>	8
Xanthid crabs	8
Amphipods	8
Copepods	8
Nebulaceans	8
Foraminifera	
<i>Calcarina</i> sp.	8
Sand grains	8

This species is common in groups of two or three over sandy-bottom areas on all reefs in water 2-30 ft deep. It reaches a large size. Its foraging habits are similar to other goatfish, consequently, polychaetes and benthonic crustaceans predominate in its diet.

Species: *Parupeneus cyclostomus* (goatfish)

Number examined: Bikini, 1; Eniwetok, 5 specimens: 2 empty

Sex: Males and females

Standard length: 130-285 mm

Digestive tract: Similar to *M. samoensis*

Food item	Percentage of fish containing the item
Crustacea	
<i>Thalamita</i> sp.	75
Xanthid crabs	25
<i>Odontodactylus</i> sp.	50
Shrimp larvae	25
Alheid shrimps	25
Amphipods	25
<i>Galathea</i> sp.	25
Fish	
Unid. fragments	50
Wrasse, small	25
<i>Calymichthys goramensis</i>	25
<i>Eriota</i> sp.	25
<i>Gnatholepis anjerensis</i>	25

This comparatively large goatfish is usually found solitary, although loose aggregations of two or three are commonly seen on all reefs with open sandy areas in water from 1-20 ft deep. It probes the bottom actively, now and then stirring up the sand to capture crustaceans hidden there. It is an active feeder on small, benthonic fish species also. Frequently rather extensive bottom areas are left "rooted" up as the result of the foraging habits of this species.

Species: *Ufeneus arge* (goatfish)

Number examined: Eniwetok, 2 specimens

Sex: Male and female

Standard length: 260-270 mm

Digestive tract: Similar to *M. samoensis*

The two specimens contained the following food items in their stomachs: Crustacea—*Thalamita* sp., *Callappa* sp., *Callianassa* sp., Unid. shrimp. This rather large species schools in groups numbering five to about 50 individuals, and frequents sandy-bottom areas on the lagoon reef in water 4-15 ft deep and on the seaward reef flat. It does not probe the sand with its barbels as do other goatfish, but rather seeks out those benthonic crustaceans living exposed on the sandy bottoms. Perhaps because it does not probe, it seems much swifter than other goatfish. Suyehiro (1942) reports that *U. bensasi* feeds rather similarly in Japan, having found alheid shrimps, amphipods, crawling shrimps (*Crago* sp.) and sand worms (*Nereis* sp.) in their stomachs.

Family Summary

Goatfish are small to medium-sized fish, some solitary, others schooling, which frequent the sandy bottom areas

of all reefs and the seaward reef flats when sufficiently covered by the rising tide. Except for the rapidly swimming *U. arge*, most busily probe the sand, moving very slowly, giving it a thorough searching for prey. Both surface benthonic forms and fossorial species are captured. In general they avoid hard-bodied fossorial forms such as clams and echinoderms because they have no crushing dentition. The teeth are mostly small and weak, restricting them to crustaceans and soft-bodied invertebrates.

Family Cirrhitidae

Species: *Amblycirrhites arcatus* (hawkfish)
Number examined: Arno, 18; Bikini, 1; Eniwetok, 1 specimen:
3 empty

Sex: Males and females
Standard length: 46-72 mm
Digestive tract: Mouth large, teeth not strongly developed; intestine short straight.

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	47
<i>Stenatherina temmincki</i>	5
Parapercid	5
Crustacean	
<i>Galathea</i> sp.	17
Xanthid crab fragments	11
<i>Thalamita</i> sp.	5
Maid crab fragments	5
<i>Trapezia</i> sp.	5
Hippolytid shrimps	5
<i>Leander</i> sp.	5
<i>Alpheus</i> sp.	5
Isopods	5

This solitary species is ubiquitous in reef areas containing large, living coral heads. It habitually lies motionless on the upper surface of living coral heads waiting for crustaceans and small fishes to come within range of its rapid thrust to capture them. It does not move much even if disturbed. Its food items are those very closely associated with living coral, hence it need not venture far away from its home base.

Species: *Paracirrhites forsteri* (hawkfish)
Number examined: Arno, 7; Bikini, 1 specimen
Sex: Females
Standard length: 50-137 mm
Digestive tract: Similar to *A. arcatus*

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	62
Wrasses, young	25
<i>Chromis caeruleus</i>	12
<i>Istiblennius</i> sp.	12
Fish eggs	12

This species has very similar habits to those of *A. arcatus*, and occupies the same general areas of the reef. Its food habits seem to run to fish rather more than to crustacea as contrasted with *A. arcatus*, but this may be the result of the larger size of *P. forsteri*. Randall (1955) reports that one of this species examined in the Gilbert Islands contained a shrimp.

Species: *Cirrhitichthys aprinus* (hawkfish)
Number examined: Arno, 3 specimens
Sex: Females
Standard length: 42-48 mm
Digestive tract: Similar to *A. arcatus*

The following food items were found in the stomachs of the three fish examined: Crustacea—Isopods, Amphipods, Crab fragments; Fish—Unid. fragments, Fish eggs; Polychaeta. This small hawkfish remains under ledges and in branching coral near the outer reef edges on both lagoon and seaward reefs, and does not lie in

exposed areas as do the two species previously mentioned. It has not been observed in the act of feeding, but apparently it takes any small forms which approach it closely enough for capture.

Species: *Cirrhitus pinnulatus* (hawkfish)

Number examined: Bikini, 1 specimen

Sex: Female

Standard length: 140 mm

Digestive tract: Similar to *A. arcatus*

The one specimen examined contained a small coral crab, *Trapezia* sp. This species resides commonly at the outer edge of the seaward reef where it lies in holes in living coral and feeds in the interstices. Similar habits for this species were mentioned by Randall (1955) for a specimen from the Gilbert Islands.

Family Summary

Hawkfish are small, solitary, demersal carnivores which lie in wait for their prey which consists mostly of crustaceans and small fish closely associated with living corals. The larger members of the family usually lie motionless on the tops and sloping sides of living coral heads, rather than partially concealed as do the small groupers. Those that lie in exposed situations are brilliantly colored and very easily seen on the coral. None are protectively or obliteratively colored, but rather appear to possess warning colors. They are sluggish when molested, moving only a few inches or a few feet. *C. pinnulatus*, however, is actually camouflaged comparable to the patterns exhibited by a scorpaenid.

Family Siganidae

Species: *Siganus rostratus* (rabbitfish)

Number examined: Arno, 2; Bikini, 3; Eniwetok, 10 specimens

Sex: Males and females

Standard length: 167-310 mm

Digestive tract: Mouth small, numerous small, conical teeth in each jaw, pharyngeal teeth well developed; stomach rather thick-walled; intestine broad, extremely long, coiled, and thick-walled

Food item	Percentage of fish containing the item
Algae	
Scraped algal filaments with calcareous powder	60
Fronds bitten off, no sand	40
Foraminifera	
<i>Calcarina</i> sp. (probably taken with scraped algae)	20

Rabbitfish are abundant on Marshallese reefs, particularly on interisland reefs and seaward reef flats during high tide, where they occur in dense schools of from 20-500 individuals. They are busy feeders, browsing head down on algal covered rocky bottoms, moving slowly along. Little attention is paid to skin-divers in the vicinity of these schools. The species is herbivorous, and may be classed as a typical browser. It, like a number of other naturally herbivorous species (Family Acanthuridae), becomes an habitué of garbage dumps where it consumes waste meat scraps. This indicates that it is not an obligatory herbivore and that both its feeding and digestive apparatus can convert to a fleshy diet on occasion.

Sueyhiro (1942), in mentioning the earlier studies of Uehida on this genus, stated that this worker had found the smaller individuals (140 mm) feeding chiefly on copepods and those from 180 to 200 mm on diatoms and seaweeds, i.e., as they grew older they turned more and more to an herbivorous diet. Sueyhiro, in his own investigation, failed to find any evidence for ascribing a carnivorous diet to the young and classed them as

herbivorous, even though some animal food was admixed with the prodigious quantities of algae eaten. Our results agree perfectly with his findings.

Family Kyphosidae

Species: *Kyphosus cinerascens* (pilot fish, rudder fish)
Number examined: Arno, 1; Eniwetok, 3 specimens; 1 contained garbage only
Sex: Males and females
Standard length: 230-345 mm
Digestive tract: Mouth small, protrusible, both jaws with a uniserial outer row of obtusely lanceolate incisors, with minute villiform teeth behind; stomach a two part gizzard; intestine very long, coiled

The specimens examined contained fronds and filaments of algae bitten off and scraped, but with no sand or calcareous powder.

This kyphosid occurred in small schools, usually swimming rapidly in mid-water or near the surface on both lagoon and seaward reefs at depths of 6-20 ft. It was especially abundant just beyond the reef edge of the seaward reefs. It is a strictly herbivorous species which may be classed as a browser.

Family Chaetodontidae

Species: *Chaetodon lunula* (butterfly fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 135 mm
Digestive tract: Mouth very small, snout somewhat produced, teeth long, slender, straight, bent at tip where they taper to a point; stomach Y-shaped, thick-walled; intestine long, coiled

The specimen examined contained many browsed tips of coral polyps. This chaetodontid was frequently observed swimming close to isolated coral heads surrounded by patches of sand. The adults were seen most commonly in the lagoon to depths of 10 feet, while the young were most abundant on the seaward reef shallows. It is a rather shy species, always turning the edge of the body to a skin-diver, so as to make it virtually impossible to spear. In confinement this species will take occasional scraps of meat, and frequently browses on algae growing on the walls of the tank.

Species: *Chaetodon citrinellus* (butterfly fish)
Number examined: Arno, 4; Bikini, 2; Eniwetok, 10 specimens
Sex: Males and females
Standard length: 39-95 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Coelenterata	
Coral polyps, no skeletal material	61
Coral polyps, some skeletal material	33
Algae	
Algal scrapings, no calcareous powder	11
Algal scrapings, with calcareous powder	5
Polychaeta	
Unid. polychaetes	5

This butterfly fish is abundant in and around coral heads at depths of 2-20 ft in the lagoon, interisland reefs, and the seaward reef. Frequently it can be seen browsing on the surface of live coral heads, particularly *Acropora* and *Porites*, where it nibbles off the small coral polyps extending from the corallites. Living coral heads placed in confinement with this chaetodontid were browsed in the same manner while under careful observation by us. The species is not restricted to a diet of polyps, however, as it is also capable of scraping fine filaments of algae off rocks and dead bases of coral

heads, as well as taking polychaetes from interstices of living coral heads.

Species: *Chaetodon ephippium* (butterfly fish)
Number examined: Arno, 4; Eniwetok 6 specimens
Sex: Males and females
Standard length: 123-160 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Coelenterata	
Coral polyps, with skeletal particles	60
Algae	
Fine filaments, no calcareous material	50
Crustacea	
Shrimp fragments	10
Polychaeta	
Unid. polychaetes	10

This species is very common around living coral on all reefs in water 2-25 ft deep. Unlike most butterfly fish, it is also commonly seen in sandy regions containing but few coral heads. Its feeding habits are similar to the chaetodontids described above.

Species: *Chaetodon vagabundus* (butterfly fish)
Number examined: Arno, 4 specimens
Sex: Males
Standard length: 58-85 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Coelenterata	
Coral polyps, with skeletal particles	75
Algae	
Fine scrapings, with calcareous powder	25
Filaments, without calcareous powder	25

This species was common only at Arno Atoll, and apparently does not occur at all, or is extremely rare, in the northern Marshall Islands. It swims about living coral on both the lagoon, and seaward reefs, and doubtless does likewise on the interisland reefs. Its food and feeding habits are similar to the chaetodontids described above.

Species: *Chaetodon reticulatus* (butterfly fish)
Number examined: Bikini, 1 specimen
Sex: Male
Standard length: 110 mm
Digestive tract: Similar to *C. lunula*, except that the teeth are very fine, numerous, flexible and brush-like

The one specimen examined contained only fine filamentous algae. This species is common on the seaward reef flats, particularly on the outer half, and in quiet waters of the lagoon rich in living coral. It habitually remains in hiding in crevices and holes in the coral. It has been observed to graze on the fine algal filaments which cover the seaward reef shallows, and apparently does not take coral polyps, at least to any great extent.

Species: *Chaetodon auriga* (butterfly fish)
Number examined: Arno, 15; Bikini, 1; Eniwetok, 13 specimens; 1 empty
Sex: Males and females
Standard length: 43-165 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	46
Coelenterata	
Coral polyps, no skeletal material	28

Algae		
Fine filaments, no calcareous powder	25	
Fine filaments, with calcareous powder	3	
Crustaceas		
Shrimp fragments	10	
<i>Alpheus</i> sp.	3	
<i>Tetralia</i> sp.	3	
Ostracods	3	
Gastropoda		
Egg masses	7	
Vermiid fragment	3	
Nemertinea	10	
Foraminifera		
<i>Calcarina</i> sp.	3	

This is a common butterfly fish on all reefs visited in water 2-25 ft in depth. It frequently is seen swimming over sandy areas near coral rubble, rather far removed from beds of living coral. Its food is more heterogeneous than other chaetodontids, although it is still classed as omnivorous. The predilection for polychaete worms noted for this species is not shared to the same extent by other members of the family. In confinement with living coral, it busily nibbles off the polyps. Its feeding habits are extremely facultative, which probably accounts for its food forays over sandy areas and in coral rubble not closely adjacent to living corals.

Species: *Megaprotodon strigangulus* (butterfly fish)

Number examined: Eniwetok, 11 specimens: 2 empty

Sex: Males and females

Standard length: 60-110 mm

Digestive tract: Similar to *C. lunula*, except that the teeth are massed toward front of jaws and protrude

All specimens with food in their stomachs contained only coral polyps with no skeletal material admixed. This species is very common on all reefs visited where living coral is abundant. It stays very close to living corals, never venturing more than a few feet away from cover. It is the only chaetodontid which seems to feed exclusively on coral polyps in nature, and its dentition is especially suited to this feeding habit. However, in confinement it will graze on encrusting algal filaments and take meat scraps.

Species: *Centropyge flavissimus* (angel fish)

Number examined: Arno, 8; Bikini, 2; Eniwetok, 2 specimens

Sex: Male and female

Standard length: 45-75 mm

Digestive tract: Snout not produced, mouth small, teeth setiform, long, flattened, tricuspid, the middle lobe much larger than the lateral lobes; intestine very long, coiled, rectum huge

These specimens had taken algae exclusively, with 88% of them biting off algal fronds which had no calcareous powder admixed, and 12% had scraped fine filaments of algae in which some calcareous powder was mixed. This angel fish is common around living coral, usually hiding in crevices or holes, on all reefs in quiet water 4-15 ft deep. It is entirely herbivorous, mostly a browser, but occasionally a grazer.

Family Summary

The chaetodontids are brilliantly colored, laterally highly compressed, deep-bodied fish as typical of coral reefs as the corals themselves. They occur singly or in pairs on both lagoon, seaward, and interisland reefs wherever coral growth is luxuriant.

Considerable heterogeneity is evident as regards the food and feeding habits of the several members of this family examined. Some appear to be rather strict herbivores, grazing or browsing short algal filaments on reef rock or on the dead bases of coral heads (*C. reticulatus* and *Centropyge flavissimus*). Others seem

to have a strong predilection for browsing and grazing off polyps of coral as well as algal filaments, and thus are omnivores (*C. citrinellus*, *C. ephippium*, *C. vagabundus*). Yet others are strictly browsers on coral polyps, and thus are carnivores (*C. lunula*, *Megaprotodon strigangulus*). Only one, *C. auriga*, is an habitual non-selective omnivore, although polychaetes comprise the bulk of its diet.

It is of interest to note, from the standpoint of feeding methods and related structural modification of the dentition, that the less specific omnivorous species which take coral polyps as part of their diet, along with algae, always contain a considerable amount of calcareous skeletal particles admixed with the food; whereas, those which are selective and consume only coral polyps do not have this admixture of calcareous skeletal material. These observations suggest that the latter species have attained a higher degree of adeptness in nibbling off the polyps. It is apparent that the omnivorous species must scrape the fine algal filaments off rocks and dead coral bases, so when taking coral polyps they probably also scrape the surface, rather than neatly biting off the polyp without touching the corallite.

To add evidence to stomach analyses and field observations on the role of chaetodontids in subsisting, in part, on living coral, several fish, *C. auriga* and *C. citrinellus*, were placed in aquaria along with living coral heads of *Acropora* sp. The fish quickly nosed down to the surface of the corallum, examined it very carefully, and then neatly nibbled off the polyps. On *Acropora* the terminal polyps on the branches were consumed first, and in a few days a great many of the polyps had been nipped off, leaving white patches on the corallum.

It was also observed that the tubular snouts of these fish were thrust into crevices and interstices in the coral possibly to secure polychaetes or small crustaceans sequestered there.

Suyehiro (1942) was rather perplexed about the food and feeding habits of *Chaetodon modestus* from Japan, and concluded that the usual food was hermit crabs and algae. No coral is available to this species, so feeding habits comparable to the Marshallese specimens would not be expected, but the omnivorous nature of *C. modestus* certainly agrees in general with our findings.

Family Acanthuridae

Species: *Acanthurus mata* (surgeon fish, tang)

Number examined: Eniwetok, 1 specimen

Sex: Undeveloped

Standard length: 390 mm

Digestive tract: Mouth small, teeth immovable, close-set, compressed, denticulate; stomach a heavy-walled gizzard; intestine thin-walled, long, coiled

This specimen had taken the following food: Algae—bitten and scraped filamentous algae from a sandy bottom, admixed with a great amount of sand and associated organisms; Foraminifera—several foraminiferans taken were probably picked up along with the sand grains while scraping algae; Gastropoda—minute gastropods, probably also taken incidental to feeding on algae growing on the sand; Detritus. This surgeon fish was commonly seen on the lagoon reef at Eniwetok in 8-10 ft of water over sandy bottoms adjacent to coral mounds. It takes immediate refuge under the coral when approached closely by a swimmer. Its feeding position is head down on compacted sandy bottoms covered with fine, filamentous algae. In the process of scraping off the algae it takes inadvertently numerous minute animals among

the benthos. *A. mata* is strictly a grazing herbivore on algal-covered, sandy bottoms.

Species: *Acanthurus xanthopterus* (surgeon fish, tang)

Number examined: Eniwetok, 4 specimens: 2 empty

Sex: Male and female

Standard length: 310-470 mm

Digestive tract: Similar to *A. mata*

The two specimens containing food in their stomachs had the following items: Algae—short, bitten off filaments with much sand; Coelenterata—Hydroid hydrocaulus; wood splinters. This species is uncommon in the Marshall Islands, but a few were observed at Eniwetok hovering over compacted sandy bottoms on the lagoon reef at depths of 4-50 ft. Its habits are very similar to *A. mata*, feeding frequently in the same area in the same manner.

Species: *Acanthurus gahhm* (surgeon fish, tang)

Number examined: Arno, 1; Eniwetok, 8 specimens

Sex: Males and females

Standard length: 170-215 mm

Digestive tract: Similar to *A. mata*

Food item	Percentage of fish containing the item
Algae	
Short, bitten off algal bases with much fine sand	100
Foraminifera	
<i>Calcarina</i> sp., probably taken incidentally to algal browsing on sand	11
Detritus, probably taken incidentally to algal browsing on sand	11

This species is abundant on all reefs with comparatively quiet water 4-40 ft deep. Large schools frequently browse over sandy bottoms, feeding on the fine, short algae growing on the compacted sand. Randall (1956) noted it to behave similarly in the Gilbert Islands.

Species: *Acanthurus olivaceus* (surgeon fish, tang)

Number examined: Arno, 7; Bikini, 1 specimen

Sex: Males and females

Standard length: 57-181 mm

Digestive tract: Similar to *A. mata*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, with calcareous powder	100
Algal scrapings, with calcareous powder	100
Coralline algae	25
Gastropoda	
Crushed small gastropods	12
Foraminifera	
<i>Calcarina</i> sp.	12

This species is common on the lagoon reefs and leeward ocean reefs in 8-25 ft of water where it swims about coral heads and coral rubble adjacent to compacted, sandy bottoms. Similar habits for this species in the Gilbert Islands were noted by Randall (1956).

During foraging periods this species may feed on the short algal cover on compacted sandy bottoms by swimming head down, or it may scrape algae from coral rubble or the dead bases of coral heads. The gastropods and foraminiferans in the stomach probably are taken inadvertently.

Species: *Acanthurus triostegus triostegus* (convict tang, manini)

Number examined: Arno, 17; Bikini, 1 specimen

Sex: Males and females

Standard length: 42-136 mm

Digestive tract: Similar to *A. mata* except that there is no gizzard, but rather a thick-walled pyloric portion of the stomach.

Food item	Percentage of fish containing the item
Algae	
Filaments bitten off, no sand or calcareous dust	100
Scraped filaments, with calcareous dust	5
Foraminifera	
<i>Calcarina</i> sp.	11
Coelenterata	
Scraped coral polyps and skeletal particles	5
Crustacea	
Copepods	5

An ubiquitous, exceedingly abundant surgeon fish on all reefs; sometimes occurring in schools of several hundred busily foraging on the algae of the reef surface. The convict tang is predominantly a browser on algal filaments growing on the reef rock or on bases of dead coral. It apparently grazes only incidentally. The animal constituents of the food probably are inadvertently taken, as this species is strictly herbivorous. Doty & Morrison (1954) report that this species characteristicly fed on non-calcareous algae covering dead coral heads (*Pocillopora* sp.) with a brown coating on the reefs of Rarotonga Atoll, Tuamotus.

The vast numbers of this species on coral reefs provide dynamic evidence of the greater efficiency in energetics for building protoplasm at the lower trophic levels of the food chain.

Species: *Acanthurus achilles* (achilles tang)

Number examined: Bikini, 1; Eniwetok, 2 specimens

Sex: Males and females

Standard length: 130-175 mm

Digestive tract: Similar to *A. t. triostegus*

All three specimens examined contained scraped filamentous algae which was not cropped closely as very little calcareous powder was present. This species is common at the outer edge of the seaward reefs where the surf is strong, and is particularly common in the surge channels. It apparently bites off algal filaments very close to the rocky base; some even appear to be scraped, but the very little calcareous powder found indicates that it is a browser rather than a grazer.

Species: *Acanthurus aequipinnatus* (surgeon fish, tang)

Number examined: Arno, 13 specimens

Sex: Males and females

Standard length: 107-162 mm

Digestive tract: Entire digestive tract thin-walled, long, coiled

All specimens examined had consumed algal fronds and filaments which were bitten off, with no sand or calcareous powder admixed. This species is uncommon and rather restricted ecologically to the outer edge of the seaward reef and to surge channels where wave action is moderate to severe. It browses on seaweeds growing in areas of luxuriant coral growth.

Species: *Acanthurus nigrofasciatus* (surgeon fish, tang)

Number examined: Arno, 21; Eniwetok, 6 specimens

Sex: Males and females

Standard length: 42-175 mm

Digestive tract: Similar to *A. mata*

Food item	Percentage of fish containing the item
Algae	
Fronds and filaments bitten off	96
Algal scrapings, with calcareous powder	11
Algal filaments, admixed with sand grains	3

This small surgeon fish is exceedingly abundant on the lagoon and interisland reefs, as well as in quiet water on the seaward reefs in depths from 2-20 feet. Schultz

et al. (1953) list this species as *elongatus*, and state that in the northern Marshall Islands it is apparently the most abundant surgeon fish on the reefs; it occurred in almost every type of habitat investigated by them. This species browses on small seaweeds primarily, but does some grazing of short filaments growing both on reef rock and on sandy bottoms. It is more characteristic of coral patches, however, than of reef flats or sandy bottoms.

Species: *Acanthurus guttatus* (surgeon fish, tang)
Number examined: Bikini, 2; Eniwetok, 3 specimens
Sex: Males and females
Standard length: 100-155 mm
Digestive tract: Stomach heavy-walled, not gizzard-like; intestine long, coiled

These specimens contained both fronds and filaments of algae which had been browsed, together with scraped algal filaments admixed with calcareous powder. Consequently, these surgeon fish both browse and graze. Randall (1955) examined several specimens and found them to contain many types of fine algae, *Jania* sp. predominating. The presence of the blue-green alga, *Calothrix*, suggested that they probably crop the algae close to the substrate. The species is abundant on the ocean reef margin, particularly in surge channels, where the current is strong and the water frequently white with bubbles. It frequently ranges up onto the seaward reef flats to forage as the tide rises.

Species: *Acanthurus lineatus* (surgeon fish, tang)
Number examined: Arno, 14 specimens
Sex: Males and females
Standard length: 142-168 mm
Digestive tract: Similar to *A. mata*

These specimens fed predominantly on algal filaments which they browsed, taking little or no calcareous material or sand. The species is, therefore, a browser, with only incidental grazing done. In the Gilbert Islands it was found to subsist mostly on finely divided red algae (Randall 1955). This surgeon fish is rare in the northern Marshall Islands, but locally abundant at Arno Atoll, where it occurred in large schools on the seaward reef flats as the tide arose. Randall (1956) reported it also abundant in the Gilbert Islands. When the seaward reef flats are largely exposed during low tide, schools of this species swim back and forth just beyond the outer reef margin.

Species: *Ctenochaetus striatus* (surgeon fish, tang)
Number examined: Arno, 12; Bikini, 2; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 118-170 mm
Digestive tract: Similar to *A. mata* except for the teeth which are long, slender, moveable and expanded at the tip

Food item	Percentage of fish containing the item
Algae	
Algal scrapings, mixed with calcareous powder	80
Algal filaments, mixed with calcareous powder	40
Algal fronds browsed, no sand or calcareous powder	6

This species was common at Arno and at Bikini Atolls, but uncommon at Eniwetok. It occurs on both the lagoon and seaward reefs in shallow water from 6-20 ft deep. It characteristically grazes by scraping dead bases of coral heads and the reef rock, but occasionally forages on the algae growing on the compacted sand adjacent to coral mounds.

Species: *Naso lituratus* (unicorn fish, surgeon fish)
Number examined: Arno, 3; Eniwetok, 6 specimens
Sex: Males and undeveloped

Standard length: 76-390 mm
Digestive tract: Mouth small, teeth bluntly rounded and close-set; stomach thin-walled; intestine long, coiled

Food item	Percentage of fish containing the item
Algae	
Fronds and filaments bitten off (mostly <i>Dictyota</i> sp.), no sand	67
Fronds and filaments bitten off, admixed with sand	33

This common species of unicorn fish frequents both quiet and turbulent water on the lagoon and seaward reefs 4-30 ft deep. It travels in small schools which browse on the larger seaweeds growing on the rocky substrate, and occasionally on the larger seaweeds growing on compacted sandy bottoms.

Species: *Naso unicornis* (unicorn fish, tang)
Number examined: Arno, 1; Eniwetok, 5 specimens
Sex: Males and females
Standard length: 298-440 mm
Digestive tract: Similar to *N. lituratus*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, no sand (<i>Dictyota</i> sp. and <i>Padina</i> sp.)	83
Fronds (<i>Dictyota</i> sp.), mixed with calcareous powder	17

This unicorn fish was common in water 3-30 ft in depth on all reefs visited. It usually occurs in small schools which swim about coral heads, especially in the deep, rocky pools on the seaward reefs. This species, like *N. lituratus*, is strictly a browser on the larger seaweeds growing on the rocky flats and coral mounds.

Species: *Zebrafoma veliferum* (surgeon fish, tang)
Number examined: Arno, 1; Eniwetok, 7 specimens
Sex: Males and females
Standard length: 140-260 mm
Digestive tract: Stomach thin-walled, no gizzard; intestine long, coiled

Food item	Percentage of fish containing the item
Algae	
Filaments bitten off and scraped, with small amount of calcareous powder	63
Fronds and filaments bitten off, no sand or calcareous powder	37

This species is especially common on the seaward reef in the surf zone, but also occurs on the interisland reefs and the quiet lagoon reefs around living coral patches. It has been observed in water 3-20 ft deep. These fish cruise slowly around coral mounds, now and then nibbling at the algal tufts growing on the bases of coral heads. Frequently, they form large schools and move onto the seaward reef flats as the tide rises. Oftentimes their dorsal fins extend out of water as they crowd each other in their foraging activities in the shallow flats. They are strictly browsers which crop seaweed rather close to its base.

Family Summary

Surgeon fishes, all herbivorous, can be segregated into three feeding types. All species have a long, coiled intestine, and a few species have a heavy-walled, muscular gizzard. The dentition is especially well suited to browsing and grazing algae.

One group, those having a well-developed gizzard (*A. mata*, *A. olivaceus*, *A. gahhm*, and *A. zanlothopterus*) are habitues of compacted sandy bottoms on which grows a carpet of short algal filaments. Each species characteristically assumes a position with its head downward and

caudal fin upward as it grazes the algal mat. Considerable sand is ingested along with the algal filaments, making the gizzard a very effective triturating organ because much of the sand is concentrated there. It is of interest to note that, although apparently distinct species, two of these gizzard-bearing surgeon fish, *A. olivaceus* and *A. gahm*, have similar color patterns, morphology, and behavior, and the other two species, *A. xanthopterus* and *A. mata*, are also exceeding similar morphologically and behavioristically. Taxonomically *A. olivaceus* and *A. gahm* have been confused, and *A. xanthopterus* and *A. mata* are rather difficult to distinguish (Randall 1956).

A second group, having no gizzard, but with essentially similar dentition, browses primarily algal fronds and filaments, with some actually grazing the rock surface for fine algal filaments. The latter group nearly always contains a small amount of calcareous powder scraped from the rock surface mixed in with the algae. Among this group, the following species are strictly browsers and rarely, if ever, have any admixed calcareous powder with the algae: *A. t. triostegus*, *A. achilles*, *A. alata*, *Naso unicornis*, and *Zebrasoma veliferum*. The following species of this group frequently do have calcareous powder admixed with the fine algal filaments, but always have much more browsed algae than that scraped while grazing: *A. lineatus*, *A. guttatus*, *A. nigroris*, and *Naso lituratus*.

The third category contains a single species, *Ctenochaetus striatus*, among the acanthurids examined. This species is strictly a grazer on very short and fine algal filaments matted on rocky surfaces. It usually always contains a large proportion of admixed calcareous powder with the algae eaten. The dentition of this species is strikingly different from other genera of surgeon fishes. The teeth which are long, movable, bristle-like, and expanded at the tips, are apparently better adapted for scraping or grazing than for biting or browsing the filaments and fronds.

There is little question that, among the fish fauna on coral reefs in the Marshall Islands, the surgeon fishes are the most important group in converting primary productivity into animal tissue. Their great abundance is ascribable only to the fact that they have more to work with than fish of higher trophic levels in regard to available potential energy, and, whether or not they attain a high percentage of efficiency in the energy transfer, they are able to convert a substantial amount of abundant plant material into fish protoplasm.

Family Scorpaenidae

Species: *Scorpaenodes parvipinnis* (scorpion fish)

Number examined: Bikini, 1 specimen

Sex: Female

Standard length: 60 mm

Digestive tract: Mouth large, teeth minute; stomach thick-walled; intestine medium-long, coiled

The single specimen examined contained an alheid shrimp in its stomach. These voracious, small carnivores are found in coral mounds almost everywhere on the reefs. They apparently conceal themselves under ledges or in the interstices of coral, lying in wait for small prey to venture close enough to be captured.

Species: *Scorpaenodes* sp. (scorpion fish)

Number examined: Bikini, 2 specimens: 1 empty

Sex: Undeveloped

Standard length: 40-75 mm

Digestive tract: Similar to *S. parvipinnis*

The single specimen containing food in its stomach had eaten several shrimps, the fragments of which remained. The habitat and behavior of this scorpion fish are similar to those described for *S. parvipinnis*.

Species: *Scorpaenopsis gibbosa* (scorpion fish)

Number examined: Arno, 2; Bikini, 1; Eniwetok, 4 specimens: 2 empty

Sex: Males and females

Standard length: 85-150 mm

Digestive tract: Similar to *S. parvipinnis*

Three of the five fish containing food had unidentified fish fragments in their stomachs, another had eaten a small wrasse, and the fifth one had consumed a small parrot fish, *Scarus* sp. This scorpion fish is a sluggish, medium-sized carnivore which lurks beneath coral heads and ledges on both interisland reef shallows and the seaward reef. It lies motionless in wait for small coral fishes and invertebrates to venture closely enough to capture. It is camouflaged as are many other fishes of a sluggish nature, but in addition bears brilliantly colored patches beneath the pectoral fins, suggestive of warning coloration. It reaches a length of about one foot, and has large, pungent dorsal spines which are probably venomous.

Species: *Pterois radiata* (turkey fish, lion fish)

Number examined: Eniwetok, 6 specimens

Sex: Males and females

Standard length: 60-100 mm

Digestive tract: Rather similar to *S. parvipinnis*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	50
<i>Stenopus hispidus</i>	16
Alheid shrimp	16
Shrimp fragments	16

Turkey fish are strikingly-colored, bizarrely-shaped scorpaenids whose sluggish habits and attractive appearance mask one of the most venomous of coral reef fishes in the Marshall Islands. They lurk beneath ledges and in crevices in luxuriant coral beds 3-15 ft deep on all reefs, and are locally very common in some areas. Their extremely poor swimming ability, the result of the highly over-developed impedimenta of the fins, would suggest that the crustaceans taken by them must venture very closely in order that capture can be made. It is not unlikely that the highly colored, greatly elongate and threadlike rays of the fins prove attractive to prey species which are captured when they come close to investigate. The turkey fish seems "aware" of its protective ability since it stands its ground when molested.

Species: *Pterois volitans* (turkey fish, lion fish)

Number examined: Eniwetok, 1 specimen

Sex: Undeveloped

Standard length: 230 mm

Digestive tract: Same as *S. parvipinnis*

The single specimen examined had eaten a bandana wrasse, *Stenopus hispidus*. The habitat and behavior of this species are essentially similar to those described for *P. radiata*. However, this species is less common, and seems more aggressive or pugnacious than *P. radiata*.

Species: *Synanceja verrucosa* (stonefish)

Number examined: Arno, 2 specimens

Sex: Males

Standard length: 110-176 mm

Digestive tract: Head broad and depressed, mouth superior, cavernous; stomach thick-walled; intestine moderately short

Both specimens examined had consumed fish which were in a late stage of digestion. This species, fortunately uncommon, is found on all reef areas where the

water is quiet. It inhabits rocky bottoms where it lies perfectly dormant for long periods of time. It is completely camouflaged because its external morphology, coloring, and shape is stonelike. Stonefish engulf small fish when they venture closely enough by a lightning-fast lunge upward while opening the cavernous mouth to draw them in. The dorsal spines are associated with poison glands and the venom, if not lethal, causes excruciating pain and serious secondary effects.

Family Summary

All scorpion fish, except *Pterois*, have essentially similar habits and feeding methods. In all cases they are sluggish, voracious carnivores, occurring solitarily under ledges or in holes where they await their prey. Except for *Pterois* and *S. gibbosa* they are well camouflaged by color and body sculpture. *S. verrucosa* attains the greatest success in this regard because it habitually lies dormant on rocky bottom and looks exactly like an algal covered rock. *P. radiata* and *P. volitans* appear to be highly colored and morphologically constructed to attract potential prey species. Their venomous spines doubtless serve them well as protection against potential enemies, as their "insolent" behavior suggests.

Family Caracanthidae

Species: *Caracanthus unicolor*

Specimens examined: Bikini, 1 specimen

Sex: Undeveloped

Standard length: 20 mm

Digestive tract: Mouth moderate in size, teeth minute; stomach large, heavy-walled; intestine short, straight

The specimen examined had eaten an alpheid shrimp. This very small species lives in the interstices of the branches of living coral, particularly *Pocillopora* spp. and *Acropora* spp., on virtually all reefs. It never ventures outside the confines of the coral head where it swims between the branches foraging for other coral-dwelling types. Alpheid shrimps would be particularly common in their diet because they also inhabit the interstices of living corals in great numbers. This caracanthid protects itself from predaceous types by bracing itself between the branches of coral with its exceedingly heavy pectorals.

Family Platyccephalidae

Species: *Thysanophrys* sp. (flathead)

Number examined: Bikini, 4; Eniwetok, 8 specimens: 5 empty

Sex: Males and females

Standard length: 82-145 mm

Digestive tract: Head depressed, mouth large, teeth villiform on jaws, canines on palatines, pharyngeal teeth large; stomach thick-walled; intestine moderately short

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	28
Xanthid crab	14
Portunid crab	14
<i>Stenorhynchus hispidus</i>	14
Shrimp fragments	14
Fish	
Unid. fragments	14

This commonly occurring, dorso-ventrally very flattened fish lies on sandy bottoms on all reef areas where it is very well camouflaged. It is a voracious carnivore which lies in wait on exposed, sandy bottoms for small crustaceans and fish to venture closely enough for capture. A rapid lunge with the enormous mouth open is sufficient to capture its comparatively slow-moving prey. In Japan the flathead, *Platycephalus indicus*, feeds ex-

clusively on benthonic fauna including small fish, crabs, polychaetes, and ophiuroids (Suyehiro 1942).

Family Pomacentridae

Species: *Abudefduf sordidus* (damsel fish)

Number examined: Arno, 9; Bikini, 2; Eniwetok, 8 specimens: 1 empty

Sex: Males and females

Standard length: 34-160 mm

Digestive tract: Mouth small, teeth incisiform, uniserial; stomach thick-walled; intestine moderately long, coiled

Food item	Percentage of fish containing the item
Algae	
Algal scrapings, with calcareous powder	38
Filaments bitten off, with sand	27
Filaments bitten off, without sand	27
Algal covered pebbles	16
Crustacea	
Crab fragments	16
Shrimp fragments	5
Isopods	5
Amphipods	5
Fish	
Unid. fragments	22
Polychaeta	
Uni. polychaetes	16
Foraminifera	
<i>Calcarina</i> sp.	16
Arachnida	
Mites	5
Coelenterata	
Hydroid fragments	5
Copepoda	
Small clam shell fragments	5
Detritus and sand	

This damsel fish was abundant on all reefs visited, particularly in the shallower portions in depths up to 6 ft. It is especially abundant in large tidepools left by the receding tide on seaward reef flats. The species is gregarious but does not form dense schools.

Its omnivorous habits are obvious from the list of food items consumed, although it is clear that algae form its principal food supply. This damsel fish apparently captures all small benthonic animals encountered while foraging on the algal-covered rocks. It is primarily a grazing species as regards its herbivorous habits. Randall (1955) reports that the one specimen examined in the Gilbert Islands had consumed green algae.

Species: *Abudefduf septemfasciatus* (damsel fish)

Number examined: Bikini, 1 specimen

Sex: Male

Standard length: 135 mm

Digestive tract: Similar to *A. sordidus*

This specimen examined contained the following food items in its stomach: Algae—Fronds bitten off, no calcareous powder; Crustacea—Palaemonid shrimp larva, Copepods; Fish—Unid. fragments.

This solitary damsel fish has habits and occupies a habitat similar to those described for *A. sordidus*. It is likewise omnivorous, although algae formed the bulk of the food in the digestive tract. Two specimens examined by Randall (1955) in the Gilbert Islands had taken only algae, primarily the fine coralline red alga, *Jania* sp.

Species: *Abudefduf leucopomus* (damsel fish)

Number examined: Bikini, 6 specimens

Sex: Males and females

Standard length: 40-55 mm

Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Scraped filaments, with much sand and calcareous powder	33
Crustacea	
Copepods, calanoid	33
Mysis	17

Fish	
Unid. fragments	33
Wrasse	17
Gastropoda	
Pteropods	17

This bright yellow damsel fish usually lives solitarily, or in groups of two or three, under rubble on reefs having a rather strong current. It appears to be a true omnivore, taking not only fine algal filaments scraped from the rubble, but also feeding in mid-water on small planktonic crustaceans, pteropods, and smaller fish.

Species: *Abudefduf saxatilis* (sergeant-major)

Number examined: Arno, 1 specimen

Sex: Female

Standard length: 88 mm

Digestive tract: Similar to *A. sordidus*

The single specimen examined contained the following items in its stomach: Algae—Filaments and fronds bitten off, no sand or calcareous powder (intestine nearly filled with algae); Crustacea—Calanoid copepods (numerous), Amphipods (numerous), Isopods (few), Ostracods (few). This species, uncommon in the Marshall Islands, usually occurs solitarily or in small aggregations at the outer edge of the sea reef and in surge channels. It feeds primarily as a browsing herbivore, but the large number of small epiphytic crustaceans leads us to suspect that these are taken more by design than by inadvertence along with the algae.

Species: *Abudefduf dicki* (damsel fish)

Number examined: Arno, 10 specimens; 1 empty

Sex: Males and females

Standard length: 60-72 mm

Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Filaments bitten off	55
Filaments scraped off	55
Fish	
Unid. fragments	22
Detritus and sand	22

This solitary damsel fish is found on all reefs with quiet water where it is associated with living corals, particularly the broad, pedestal colonies of *Acropora reticulata* and the staghorn corals representing several species of *Acropora*. It is not at all demersal and swims mostly in mid-water or near the surface. The browsing herbivorous habits of this species predominate, but it is an opportunistic species which will take smaller fish and doubtless swimming invertebrates which venture near it.

Species: *Abudefduf biocellatus* (damsel fish)

Number examined: Arno, 21; Eniwetok, 1 specimen

Sex: Males and females

Standard length: 47-68 mm

Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, no calcareous powder	33
Filaments scraped off, much calcareous powder	33
Fronds bitten off, admixed with sand	28
Crustacea	
Isopods	9
Cyclopoid copepods	4
Fish	
Unid. fragments	9
Fish eggs	4
Polychaeta	9
Foraminifera	
Calcarina sp.	4

According to some authors (Schultz 1943, Strasburg 1953, Randall 1955) the specimens included under *biocellatus* in this report probably represent a complex of two species, *biocellatus* and *zonatus*. However, it is also possible that *zonatus* may be just a color variant. It is of interest to note that the form considered *biocellatus* abounds in shallow water in depths up to 6 ft on all reefs where rubble is predominant. It prefers hard, conglomerate bottoms, taking refuge under reef rubble when disturbed, and is rarely if ever seen over sandy bottoms. On the other hand, the form referred to as *zonatus* is usually found over sandy bottoms and nowhere else. Because of these different habits Randall (1955) separated the species in his report on fishes of the Gilbert Islands, although he found *biocellatus* only in outer reef areas where coral was abundant. Regardless of the ultimate taxonomic disposition of these species, the food and feeding habits reported here will serve for one or both species. These damsel fish are usually solitary, but sometimes form loose aggregations of two or three individuals. They are primarily herbivores which both browse and graze algae growing on rubble or compacted sand. The cyclopoid copepods, fish fragments, and polychaetes in their diet indicate that they are facultative omnivores as well.

Species: *Abudefduf amabilis* (damsel fish)

Number examined: Arno, 13; Bikini, 5 specimens

Sex: Males and females

Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Filaments scraped off, much calcareous powder	38
Fronds bitten off, no sand or calcareous powder	33
Filaments admixed with sand grains	22
Coralline algae	5
Foraminifera	
Calcarina sp.	16
Fish	
Unid. fragments	5
Polychaeta	
Unid. fragments	5

This species occurs in groups of 2-3 individuals primarily on the seaward reef flats in 1-3 ft of water. It is also common on interisland reefs. It prefers areas where the water is in motion, particularly in the area of waves of translation coming across the seaward reef flats on an incoming tide. It will take refuge under pieces of reef rubble. *A. amabilis* may be designated a grazing herbivore primarily on fine algae covering reef rock, although it does browse at times. Like many other damsel fish it is a facultative omnivore.

Species: *Abudefduf glaucus* (damsel fish)

Number examined: Arno, 26; Bikini, 6 specimens

Sex: Males and females

Standard length: 46-75 mm

Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, admixed with sand grains	78
Fine filaments, without sand grains	3
Scraped filaments, with calcareous powder	6
Crustacea	
Shrimp fragments	28
Tetralia globerrima	6
Isopods	3
Amphipods	3

Fish	
Unid. fragments	12
Eggs of <i>Istiblennius</i> sp.	6
Unid. goby	3
Polychaeta	
Unid. polychaetes	3
Gastropoda	
<i>Cerithium</i> sp.	3
Insect	
Winged ant	3

This common grey or blue damsel fish occurs solitarily or in groups of 2-3 individuals on almost all shallow areas of the reefs where the water is about 3-4 ft deep. It is most prevalent over hard rocky bottoms, and often seeks refuge below large reef rocks. Although it is primarily a grazing herbivore scraping off fine filaments of algae growing on rock surfaces, it very readily becomes a facultative carnivore taking small crustaceans and benthonic forms. The presence of trapezoid crabs and shrimps in about one-half of the specimens examined indicates that they actively seek these forms from the interstices of living heads of branching *Acropora* sp.

Species: *Abudefduf lacrymatus* (damsel fish)
Number examined: Arno, 10; Eniwetok, 4 specimens
Sex: Males and females
Standard length: 39-67 mm
Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, with few sand grains	57
Fine filaments, with no sand grains	42
Foraminifera	
<i>Calcarina</i> sp.	14
Unid. species	7
Crustacea	
Copepods	14
Gastropoda	
Crushed small gastropods	7
Fish	
Fish eggs	7

This solitary damsel fish is shy and seen only occasionally despite the fact that it is one of the commonest in shallow reef areas in and around living coral where the water is from 3-12 ft deep. It forages as a browsing herbivore predominantly, with copepods and foraminifera, and possibly even fish eggs and small gastropods, being picked up inadvertently with algae. The crushed gastropods are difficult to explain because the species possesses no dental armature capable of crushing action. Since they are primarily thin-shelled, epiphytic types, it is probable that they were bitten while the fish browsed on the algae.

Species: *Chromis atripectoralis* (coral fish)
Number examined: Eniwetok, 24 specimens: 2 empty

Sex: Males and females

Standard length: 50-68 mm

Digestive tract: Mouth small, teeth with outer row of short canines with two enlarged near symphysis of lower jaw, inner row of teeth villiform; stomach very large, thin-walled; intestine short, straight

Food item	Percentage of fish containing the item
Crustacea	
Copepods	85
Shrimp nauplii	61
Small shrimps	33
Mysids	61
Crab zoeae	33
Fish	
Larval fish	4
Polychaeta	
Polychaeta larvae	4
Algae	
Fronds bitten off	4

These brilliant blue coral fish form dense schools about larger branching coral heads, particularly *Pocillopora* sp. and branching *Acropora* sp., in quiet water of the lagoon and leeward ocean reefs. They venture from the coral heads about 3-6 ft, frequently forming a "cloud" of fish about them.

Observations of these schools show the fish to be exceedingly busy capturing small plankters which swarm in the quiet waters of the reefs. The food analysis indicates that copepods, mysids, and shrimp nauplii are most commonly taken, and these can be observed to be the most abundant planktonic food available to them. Although they consume zooplankton, they are not plankton feeders in the sense that they possess structural features which enable them to sieve plankton from the water, but rather represent a carnivorous type which selects particular kinds of plankters which it catches one at a time through visual contact.

Species: *Chromis caeruleus* (coral fish)
Number examined: Arno, 11 specimens: 1 empty
Sex: Males and females
Standard length: 32-49 mm
Digestive tract: Similar to *C. atripectoralis*

Food item	Percentage of fish containing the item
Fish	
<i>C. caeruleus</i> eggs	60
Crustacea	
Calanoid copepods	50
Cyclopoid copepods	30
Metanauplii	20
Ostracods	20
Crab zoeae	10
Isopods	10
Sand grains	10

This species, like *C. atripectoralis*, occurs in comparatively large schools in and about interstices of branching corals, particularly *Acropora* sp., in the case of *C. caeruleus*. They are found wherever such corals occur in the quiet waters of the lagoon, interisland, and seaward reefs. Food habits and feeding methods for this species are rather similar to those of *C. atripectoralis*, in that they are a small, mid-water carnivore which feeds primarily on the crustacean elements of the zooplankton in and near the branching corals. It is of interest to note that over one-half of the specimens examined had eaten eggs spawned just previously. All females were gravid and spawning was in full swing. It is not unusual for fish to eat the eggs they have just spawned, and here is a good example of this phenomenon.

Species: *Dascyllus aruanus* (coral fish)
Number examined: Arno, 22 specimens
Sex: Males and females
Standard length: 32-51 mm
Digestive tract: Mouth small, teeth similar to *C. atripectoralis*; stomach thick-walled; intestine medium long, coiled

Food item	Percentage of fish containing the item
Crustacea	
Calanoid copepods	72
Copepod metanauplii	36
Cyclopoid copepods	27
Isopods	36
Crab zoeae	22
Shrimp fragments	9
Ostracods	9
Fish	
Fish eggs	45
Unid. fragments	22
Gobies	4
Polychaeta	
Unid. fragments	18
Algae	
Filaments bitten off	59
Filaments scraped, some calcareous powder	4

Frequently large numbers of this species aggregate in branching corals, particularly in *Pocillopora* sp. and *Stylophora* sp. They occur on all reefs where the water is relatively quiet down to a depth of about 15-20 ft. As a swimmer approaches they sink down into the interstices of the coral, remaining there even if the coral head is torn loose and carried ashore. The species is omnivorous, favoring, perhaps, animal food over plant food, but taking a sufficient amount of each to be definitely classed as omnivorous. Its food items are taken both from the mid-water fauna and from the surface of the living coral head and its dead base. The fish eggs taken were spawned in the interstices of the coral, probably by this species itself, although other species place their eggs in such locations.

Species: *Pomacentrus pavo* (damsel fish)

Number examined: Arno, 20 specimens

Sex: Males and females

Standard length: 32-63 mm

Digestive tract: Mouth small, teeth in one series, incisiform; stomach small, heavy-walled; intestine long, coiled

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	40
Fish eggs	40
<i>Apogon novemfasciatus</i>	5
Fish scales	5
Crustacea	
Copepods	35
Copepod metanauplii	5
Shrimp fragments	15
Ostracods	10
Isopods	5
Crab <i>zeae</i>	5
Algae	
Fine filaments, no sand or calcareous powder	10

This more or less solitary pomacentrid is closely associated with living coral mainly in the quiet waters of lagoons at depths of 4-25 ft. Only a few individuals are associated with any one coral head. Although other pomacentrids examined were almost entirely herbivorous, this species is just the reverse and is almost exclusively a carnivore preying upon small fish, crustaceans, and polychaete worms taken either from the mid-water zooplankton or from the interstices of the coral in which it lives. Its rather typical herbivorous-type digestive tract is an enigma.

Species: *Pomacentrus nigricans* (damsel fish)

Number examined: Arno, 19 specimens

Sex: Males and females

Standard length: 52-79 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, with sand grains	63
Algal scrapings, with calcareous powder	31
Algal fronds bitten off, no sand or powder	31
Fish	
Unid. fragments	5

P. nigricans is a very abundant species in shallow water around living coral on almost all reefs, where it lives in crevices in the coral. It exhibits very strong territorial tendencies. This species is almost exclusively a grazing herbivore taking fine filaments from the compacted sand surface adjacent to coral patches. The fact that some specimens had fish fragments remaining in the stomach indicates that they can be omnivorous at times.

Species: *Pomacentrus jenkinsi* (damsel fish)

Number examined: Arno, 21 specimens

Sex: Males and females

Standard length: 53-83 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, no sand grains	80
Fine filaments, with sand grains	14
Algal scrapings, with calcareous powder	9
Fish	
Unid. fragments	9
Fish eggs	4

This species is rather uncommon in the northern Marshall Islands, but common at Arno Atoll in the southern Marshalls. It frequents branching corals, either dead or alive, in quiet water of the lagoon and leeward ocean reef shallows to a depth of about 6 ft. It is predominantly a browser on fine algal growth, but grazes at times. It will take animal food as evidenced by its ingestion of both fish eggs and small fish. Its animal food habits are certainly comparatively insignificant.

Species: *Pomacentrus albofasciatus* (damsel fish)

Number examined: Arno, 22 specimens

Sex: Males and females

Standard length: 48-70 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, with admixed sand grains	81
Algal scrapings, with calcareous powder	22
Fine filaments, with no sand grains or powder	4
Crustacea	
Shrimp fragments	4
Fish	
Fish eggs	4

This species, common at Arno Atoll, was uncommon in the northern Marshall Islands. It occurs solitarily or in small groups in reef shallows near coral patches where the water is quiet in depths from 3-12 ft. The great quantity of sand admixed with the algae in the digestive tract clearly indicates that this species is a grazer of fine algal filaments on compacted sandy bottoms where it apparently crops very closely, and gets large quantities of sand along with the algae. It also grazes on rocks and dead coral surfaces. Like other pomacentrids it can be a facultative omnivore and takes small crustaceans on occasion.

Species: *Pomacentrus raiuli* (damsel fish)

Number examined: Arno, 8; Eniwetok, 12 specimens

Sex: Males and females

Standard length: 34-61 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, no sand grains	75
Scraped filaments, with calcareous powder	15
Fish	
Unid. fragments	10
Fish eggs	10
Crustacea	
Copepods	10
Amphipods	5
Polychaeta	5

This solitary species lives in crevices and is abundant about living coral patches in water 4-15 ft deep on all reefs. Although it is primarily a browsing herbivore, it frequently behaves omnivorously, and takes small fish and invertebrates occurring in the branching coral heads where it lives.

Family Summary

The pomacentrids are ubiquitous, usually brilliantly colored, coral fishes characteristic of coral reefs in almost every environment found there. Many are solitary, some form small aggregations, while others occur in dense aggregations which have the cohesive and integrated characteristics of highly developed schools. Almost all of them, particularly the aggregating species, are closely associated with, even ecologically bound to, giant heads of branching corals.

The food habits within the family, and even the structural anatomy of the digestive tract, are quite variable, and it is difficult to segregate them into discrete groups of homogeneous habits as regards food and feeding proclivities. They range from almost exclusive herbivores to exclusive carnivores, with most of the species pursuing an omnivorous life to a greater or lesser degree.

Among those species which feed primarily on algae, both by browsing and grazing with approximately equal facility are *A. dicki*, *A. biocellatus*, *A. amabilis*, *A. glaucus*, *A. lacrymatus*, *P. vauili*, *P. albofasciatus*, *P. jenkinsi*, and *P. nigricans*. In every case these species consumed some animal types.

One species, *P. pavo*, is almost exclusively carnivorous, taking fish and crustaceans primarily. This is a solitary species which swims about small boulders and coral mounds on the lagoon reef.

Among the omnivores which take animal food both from mid-water and bottom are *A. septemfasciatus*, *A. leucopomus*, *A. saratilis*, and *A. sordidus*. Of these, *A. sordidus* is the most completely omnivorous species, taking all types of food. It is abundant on the seaward reef flats and in intertidal pools, in aggregations which are not well enough integrated to qualify as schools.

The three species which feed on zooplankton (*C. caeruleus*, *C. atripectoralis*, and *D. aruanus*) are characteristic dwellers in large, branched coral heads. Often as many as 500-1000 fish of *caeruleus* and *atripectoralis* may aggregate in and about one of these giant, ramose heads. When disturbed, they swim down amongst the branches of the coral, but normally the swarm of fish extends several feet outward from the head. *D. aruanus*, while exhibiting habits similar to *Chromis*, occurs in much smaller aggregations and in smaller ramose heads. The plankton taken by these species are not sieved out of the water by any special device, but rather are captured individually on sight. These plankters form swarms over the reef shallows in quiet water.

The dentition of the feeders on plankton is somewhat different from that of the herbivorous or omnivorous feeders. The teeth of the former types are conical and widely spaced, whereas the teeth of the fish belonging to the other genera, *Abudefduf* and *Pomacentrus*, are villiform or incisiform in bands. The latter are adapted for biting (browsing) or scraping (grazing), just as were the teeth of the herbivorous surgeon fishes.

Family Labridae

Species: *Epibulus insidiator* (wrasse)
Number examined: Bikini, 1; Eniwetok, 1 specimen
Sex: Undeveloped

Standard length: 125-130 mm
Digestive tract: Mouth not produced, but highly protrusive, jaws extending backward beneath head; canines at symphyses of jaws; stomach thick-walled; intestine short

Both specimens examined had eaten alheid shrimps. This species is not common and those taken were from

the seaward reef in channels containing living coral. It doubtless occurs elsewhere on the reefs, particularly in coral patches on interisland reefs. This wrasse habitually feeds in ramose corals by extending its exceedingly protractile snout into the interstices to capture small alheid shrimps and xanthid crabs living there.

Species: *Gomphosus varius* (wrasse)

Number examined: Arno, 3; Bikini, 4; Eniwetok, 14 specimens
1 empty

Sex: Females

Standard length: 58-120 mm

Digestive tract: Snout produced, tubular; canines at symphyses of jaws; stomach thick-walled; intestine short

Food item	Percentage of fish containing the item
Crustacea	
Alheid shrimps	40
Shrimp fragments	20
Xanthid crab fragments	35
<i>Trapezia</i> sp.	5
Pelecypoda	
Unid. small clam	5
Gastropoda	
Unid. small gastropods	5
Fish	
Unid. fragments	5
Algae	
Fronds, bitten off	5

This species has recently been combined with *G. tricolor*, with the latter referred to synonymy (Strasburg & Hiatt 1957). Although we did not examine the food of the males of this species (formerly designated *G. tricolor*), it may be assumed that the food predilections are the same as for the females examined by us. Randall (1955) examined two males (= *G. tricolor*) in the Gilbert Islands and found them to contain stomatopods and alheid shrimps, crustaceans characteristic of branching corals.

These wrasses are uncommon but widely distributed about all reefs with living coral in water up to a depth of about 35 ft. They are more common on lagoon reefs, than elsewhere, usually swimming solitarily with characteristic oar-like movements of the pectoral fins. Their long snout is an effective device for probing into interstices of ramose corals where their crustacean prey conceal themselves.

Species: *Pseudocheilinus hexataenia* (wrasse)

Number examined: Arno, 5; Eniwetok, 4 specimens

Sex: Males and females

Standard length: 38-57 mm

Digestive tract: Mouth small, canines on each side of symphyses, upper pair long, curved outward and backward; stomach heavy-walled; intestine medium long

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	22
Copepods	44
Ostracods	11
Isopods	11
Foraminifera	
<i>Calcarina</i> sp.	44
Unid. foraminiferans	11

This small wrasse is common in all living coral patches on all reefs in water 3-10 ft deep. It lives solitarily among the branches of ramose corals and feeds primarily on the benthonic fauna living on rubble and sandy bottoms adjacent to coral patches. The specimens examined at Arno contained only the foraminiferan, *Calcarina* sp., and the stomach and gut were crammed full. It was noted then that this species was probably a selective feeder on *Calcarina* sp., but none of these foraminiferans were found in the digestive tracts of specimens examined from Eniwetok. The latter fish had taken only small, benthonic crustaceans. Our data

indicate that this species is probably non-selective among the benthonic fauna, but feeds exclusively on certain abundant, easily available forms.

Species: *Labroides dimidiatus* (wrasse)
Number examined: Arno, 1; Eniwetok, 4 specimens

Sex: Females and undeveloped

Standard length: 54-68 mm

Digestive tract: Deep notch at middle of lower lip with fleshy horn extending forward on each side of lower jaw forming lips; pair of large canines at front of each jaw separated by small teeth at symphyses; stomach thin-walled, large; intestine short, nearly straight

Food item	Percentage of fish containing the item
Crustacea	
Calagoid copepods	80
Copepods, free-living	40
Mysids	20
Fish	
Fish scales	20

This solitary, agile, strikingly-colored fish is common on all reefs around living coral to depths of about 15 ft. Its peculiar habits which attract the attention of a skin-diver have been noted by several authors. Randall (1955) states, "It often exhibited an unusual mode of swimming by oscillating the posterior part of the body up and down as if to attract attention. It was seen to dance around other fishes in this manner and to pick at their bodies. The fishes receiving such attention often slowed their swimming or came to a stop. It was thought at the time that the *Labroides* were picking off external parasites from these fishes. The gut contents of two specimens from the Gilbert Islands and three from the Marshall Islands consisted of calagoid copepods and a few fish scales. The two remaining Gilbert Islands specimens had eaten tiny isopods along with several fish scales."

Our results fit closely with those obtained by Randall, indicating that the parasitic copepod "picking" from other fish is its predominant mode of feeding, but that it can also take other mid-water plankters. The role of the cleft lower jaw in feeding is not understood. Smith (1953) refers to this species in African waters as one which feeds on minute organisms on rocks, and has been observed to nibble over the mouthparts and gill-covers of large rock-eels.

Species: *Noraculichthys taeniourus* (wrasse)

Number examined: Eniwetok, 1 specimen

Sex: Female

Standard length: 102 mm

Digestive tract: Mouth moderately small, canines at symphyses of both jaws; stomach not well-defined; intestine short, almost straight

The single specimen examined contained an alpheid shrimp in its stomach. This is an uncommon species which occurs solitarily on almost all sandy-bottomed and rubble-strewn reefs at depths of 4-20 ft. It seldom ventures more than a few feet from bottom rubble which serves it as shelter, and is never seen around living coral.

Species: *Stethojulis axillaris* (wrasse)

Number examined: Arno, 17; Eniwetok, 4 specimens

Sex: Males and females

Standard length: 44-75 mm

Digestive tract: Mouth moderately small, no canine teeth, small incisiform teeth in sides of jaws, pharyngeal teeth strong, rounded; stomach not well-defined; intestine rather short

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	61
Crustacea	
Cyclopoid copepods	38
Calanoid copepods	19
Harpacticoid copepods	9

Copepod metanauplii	14
Cypris larvae	14
Isopods	33
Shrimp fragments	33
Ostracods	19
Xanthid crab fragments	14
Foraminifera	
<i>Calcarina</i> sp.	23
Gastropoda	
Unid. small gastropods	4
Algae	
Fine filaments with sand grains	14
Sand grains	19

This extremely abundant labrid occurs solitarily in shallow water on nearly all reefs. It lives along the bases of coral mounds and patches adjacent to sandy bottoms. It is obviously a non-selective carnivore which forages mostly on the benthonic fauna of sandy areas. It does, however, take some planktonic copepods which it must capture in mid-water.

Species: *Stethojulis* sp. (wrasse)

Number examined: Eniwetok, 6; Arno, 5 specimens

Sex: males and undeveloped

Standard length: 70-95 mm

Digestive tract: Similar to *S. axillaris*

Food item	Percentage of fish containing the item
Crustacea	
Isopods	72
Copepods	54
Cypris larvae	9
Ostracods	45
Shrimp fragments	27
Crab zoeae	9
Gastropoda	
Crushed small gastropods	45
Polychaeta	
Unid. polychaetes	18
Foraminifera	
Unid. foraminiferans	18
Pelecyopoda	
Crushed small clams	9
Algae	
Filaments scraped, with sand grains	18
Sand grains	81

This species is common on nearly all reefs where it lives, solitarily, around living coral patches adjacent to sandy and rubble-strewn bottoms. It forages for both benthonic and fossorial invertebrates on sandy bottoms, taking primarily crustaceans and polychaetes. The heavy molariform, pharyngeal dentition enables it to crush small hard-bodied species.

Species: *Halichoeres hoevenii* (wrasse)

Number examined: Arno, 1; Eniwetok, 3 specimens

Sex: Female

Standard length: 54-66 mm

Digestive tract: Snout rather pointed, mouth small; symphyses of lower jaw with 1 pair of canines, upper jaw with 2 pairs, pharyngeal teeth molar-like; stomach not well-defined; intestine short

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	75
Crustacea	
Copepods	50
Isopods	50
Foraminifera	
<i>Calcarina</i> sp.	25
Algae	
Fine filaments of green and coralline algae with much calcareous powder	50

This wrasse is uncommon and is found only in quiet water on the lagoon and leeward ocean reefs at depths of 6-20 ft. It darts about coral heads and usually stays close to the bases of large coral mounds in the lagoon. At Arno Atoll, the single individual examined contained only the foraminiferan, *Calcarina* sp., with which its gut

was crammed. However, at Eniwetok different food habits prevailed, with no *Calcarina* taken at all.

Species: *Halichoeres marginatus* (wrasse)
Number examined: Eniwetok, 5 specimens
Sex: Females
Standard length: 48-88 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Crustacea	
Isopods	80
Copepods	60
Polychaeta	
Unid. polychaetes	60
Gastropoda	
Crushed gastropods	20
Foraminifera	
Large foraminiferans	20
Algae	
Fine filaments scraped, with sand grains	20

This solitary species is common among luxuriant coral patches in shallow areas on all reefs. It characteristical- ly swims around the top sides of coral heads, only rarely taking refuge when molested. *H. marginatus* may be classed as a benthonic carnivore which usually forages on compacted sandy bottoms, taking mostly small crustaceans and polychaete worms. The algae may have been taken inadvertently during its foraging activities for benthonic fauna in the algal-covered substrate. Its molariform pharyngeals are responsible for crushing the shells of gastropods.

Species: *Halichoeres hortulanus* (wrasse)
Number examined: Arno, 5; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 69-230 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Gastropoda	
Crushed gastropods	100
Polychaeta	
Unid. polychaetes	33
Fish	
Unid. fragments	33
Crustacea	
Fragments	17
Hermit crabs, shells crushed	17
Pelecypoda	
Sand-dwelling clams, crushed	17
Algae	
Fine filaments	17

This species is solitary and uncommon, but occurs on all reefs with living coral heads or coral mounds in depths from 3-15 ft. It is a rapid swimmer, seldom taking cover. The food taken indicates that it forages for benthonic and fossorial species, especially hard-bodied forms which it crushes with its heavy pharyngeal teeth. Its primary food consists of small sand-dwelling gastropods, and, in the process of capturing these, it undoubtedly takes many hermit crabs occupying gastropod shells. The shell-crushing habits of this genus are also mentioned by Suyehiro (1942) in his account of *H. poecilopterus* in Japan which bites off barnacles and mussels and then crushes them with its pharyngeal teeth.

Species: *Halichoeres trimaculatus* (wrasse)
Number examined: Arno, 24; Bikini, 6; Eniwetok, 2 specimens
Sex: Males and females
Standard length: 42-120 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Crustacea	
Hermit crab fragments, crushed	83
Shrimp fragments	25
Xanthid crab fragments	12

Stomatopod fragments	6
Amphipods	3
Copepods	3
Fish	
Unid. fragments	9
Fish eggs	9
Apogon novemfasciatus	3
Foraminifera	
Calcarina sp.	6
Polychaeta	
Unid. polychaetes	3
Pelecypoda	
Crushed clams	3
Amphineura	
Solenogastrid chiton	3
Algae	
Fine filaments, with sand grains	6

This is the most abundant wrasse on all reefs, partic- ularly favoring sandy bottoms with scattered rubble for cover. It will actually burrow under the sand if molested. Like the other members of this genus, this species is carnivorous on benthonic and fossorial fauna. It has a predilection for hermit crabs which it secures by crushing their shells with the heavy pharyngeal molars. Virtually any prey occurring on sandy bottoms is taken by this fish.

Species: *Halichoeres margaritaceus* (wrasse)
Number examined: Arno, 15 specimens
Sex: Males and females
Standard length: 40-86 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	46
Tanaid isopods	20
Xanthid crab fragments	13
Trapezia sp.	6
Foraminifera	
Calcarina sp.	26
Polychaeta	
Unid. polychaetes	26
Mollusca	
Crushed gastropods	13
Chiton fragments	6
Fish	
Unid. fragments	6
Fish eggs	6

This wrasse is a very abundant, solitary species which occurs in shallow water on all reefs. It is especially abundant at the outer edge of the seaward reefs and in the surge channels. In the lagoon it is found commonly around coral patches 15-20 ft deep. This wrasse feeds less often on sandy bottoms than the other members of the genus examined, and more on and in ramose corals. However, it still is predominantly a feeder on benthonic fauna, but takes no fossorial species as other members of the genus do.

Species: *Macropharyngodon meleagris* (wrasse)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 70 mm
Digestive tract: Mouth small, 2 pairs of canines at symphyses of upper and lower jaws, strong canines at corner of upper jaw, pharyngeal teeth molariform; stomach not well-defined; intestine short

The single specimen examined had a crushed rock-dwelling gastropod in its stomach. This small wrasse swims rapidly about coral heads, taking refuge in ramose types in quiet waters of the lagoon and seaward reefs in depths to about 6 feet. It evidently forages on and in coral heads and rocks.

Species: *Macropharyngodon pardalis* (wrasse)
Number examined: Arno, 1; Eniwetok, 3 specimens
Sex: Males and undeveloped
Standard length: 43-57 mm
Digestive tract: Similar to *M. meleagris*

Food item	Percentage of fish containing the item	Food item	Percentage of fish containing the item
Gastropoda		Species: <i>Thalassoma hardwickei</i> (wrasse)	
Crushed rock-dwelling gastropods	75	Number examined: Arno, 7; Eniwetok, 4 specimens	
Foraminifera		Sex: Females	
<i>Calcarina</i> sp.	25	Standard length: 35-100 mm	
Unid. foraminiferans	25	Digestive tract: Similar to <i>T. umbrostygma</i>	
Sand grains	25		

This small, solitary species is very common over living coral on leeward ocean reefs and lagoon reefs in water 3-5 ft deep. It secludes itself in crevices in coral. The Arno specimen had fed exclusively on foraminiferans characteristic of sandy bottoms; whereas, the Eniwetok specimens fed exclusively on rock-dwelling gastropods which were crushed by the heavy pharyngeal teeth. It would appear that this species forages either on sand or rock bottoms, taking hard-bodied species which it can crush.

Species: *Thalassoma umbrostygma* (wrasse)

Number examined: Bikini, 2 specimens

Sex: Male and female

Standard length: 160 mm

Digestive tract: Mouth small, 1 pair canines at symphyses of jaws, pharyngeals molariform; stomach large, thin-walled; intestine short, straight

One of the specimens examined contained an unidentified fish, the other a stomatopod, *Odontodactylus* sp. This solitary wrasse is most common at the seaward reef front and in the back-ridge trough. It also occurs in the interisland reef shallows about living coral. Randall (1955) reported that this species consumed small crabs in the Gilbert Islands.

Species: *Thalassoma quinquevittata* (wrasse)

Number examined: Arno, 20; Eniwetok, 3 specimens

Sex: Males and females

Standard length: 49-184 mm

Digestive tract: Similar to *T. umbrostygma*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	52
Shrimp fragments	13
<i>Trapezia</i> sp.	4
Fish	
Unid. fragments	21
<i>Apogon novemfasciatus</i>	8
Gastropoda	
Crushed gastropods	4
Echinodermata	
Echinoid fragments	4
Coelenterata	
Tip of <i>Pocillopora damicornis</i> , partially digested	4
Algae	
Short clumps	4

This wrasse is very abundant on all reefs around living coral and rocky rubble to depths of about 15 ft. Like other wrasses, it is solitary. Its consumption of crustaceans which live in the interstices of living coral, a coral-dwelling cardinal fish, and the tip of a ramose coral indicates that coral heads and their bases are its primary foraging areas.

Species: *Thalassoma lucasanum marnae* (wrasse)

Number examined: Eniwetok, 2 specimens

Sex: Undeveloped

Standard length: 44-50 mm

Digestive tract: Similar to *T. umbrostygma*

The two specimens examined contained the following food items: Crustacea—Shrimp larvae, Mysids, Crab zoeae, Copepods. This small common species swims rapidly about large lagoon coral heads in quiet water 3-10 ft deep. It feeds mostly on the abundant plankters in the vicinity.

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	36
Crab zoeae	18
Crab megalopa	9
Shrimp larvae	18
Hippolytid shrimp fragments	9
Copepods	18
Isopods	9
Fish	
Unid. fragments	27
Belonid	9
Foraminifera	
Several species of pelagic foraminiferans	9

This wrasse is common on all quiet reef areas near living coral where it swims solitarily and actively about the tops and sides of the coral heads. The food consumed suggests that it feeds in and about living corals, at times taking small plankters in mid-water. The small belonid fish among the food items indicates that it is a predacious carnivore.

Species: *Thalassoma lutescens* (wrasse)

Number examined: Arno, 1; Eniwetok, 9 specimens

Sex: Females and undeveloped

Standard length: 57-105 mm

Digestive tract: Similar to *T. umbrostygma*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crabs	30
<i>Tetralia globerrima</i>	10
Shrimp fragments	30
Alpheid shrimp fragments	10
Gastropoda	
Unid. crushed gastropods	20
<i>Atys</i> sp., crushed	10
Polychaeta	
Unid. polychaetes	10
Pelecypoda	
<i>Arca</i> sp., crushed	10
Echinodermata	
Ophiuroid fragments	10
Echinoid fragments	10
Algae	
Fine filaments scraped off	30
Fine scrapings, with calcareous powder	10

This bright yellow, solitary wrasse is common on all shallow reef areas near living coral. It is particularly common in the lagoon around living coral patches where it swims rapidly about the tops and sides of the coral heads. This species exhibits quite heterogeneous carnivorous activities, feeding sometimes in amongst the ramose corals for small coral-dwelling crustaceans, and at other times apparently taking benthonic species from the sandy bottom. The algae contained in the stomach may possibly be the inadvertent result of foraging for benthonic gastropods and polychaetes.

Species: *Cheilinus oxycephalus* (wrasse)

Number examined: Eniwetok, 5 specimens

Sex: Females and undeveloped

Standard length: 65-75 mm

Digestive tract: Mouth small, 1 pair of canines at symphyses of upper and lower jaws, pharyngeal teeth heavy, molariform; stomach virtually absent; intestine short, nearly straight

Food item	Percentage of fish containing the item
Crustacea	
Alpheid shrimp fragments	75
Crab fragments	25
Amphipods	25
Gastropoda	
Small gastropods	50

This is an abundant, medium-sized, solitary wrasse which occurs on all reefs with quiet water. It hides under coral or rocks. It is carnivorous, taking crustaceans living in corals and gastropods frequenting corals and coral mounds.

Species: *Cheilinus chlorourus* (wrasse)
Number examined: Arno, 7 specimens: 1 empty
Sex: Males and females
Standard length: 44-98 mm
Digestive tract: Similar to *C. oxycephalus*

Food item	Percentage of fish containing the item
Gastropoda	
Whole or crushed gastropods	66
Crustacea	
Shrimp fragments	50
Polychaeta	
Unid. polychaetes	17
Insecta	
Beetles	17

This is a common, solitary wrasse which is found on all reefs about living coral or rubble. It is a slow swimmer compared to many other wrasses in the same habitat. *C. chlorourus* is carnivorous, subsisting primarily on small gastropods taken from coral heads or the rocky bottom nearby. Most specimens had the lower part of the intestine filled with a solid bolus of gastropod shell fragments.

Species: *Cheilinus trilobatus* (wrasse)
Number examined: Arno, 14; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 74-270 mm
Digestive tract: Similar to *C. oxycephalus*

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	59
<i>Apogon novemfasciatus</i>	6
Crustacea	
Crab fragments	40
Hermit crabs	6
Shrimp fragments	26
Gastropoda	
Crushed shells, <i>Cerithium</i> sp.	18
Pelecypoda	
Crushed clams	6
Algae	
Small fragments of rock containing algal fronds and filaments	6

This solitary wrasse is common on all reef areas around living coral or rubble, under which it lives. It frequently is seen hovering over the sandy bottom near its shelter. This species is carnivorous, taking fish, crustaceans, and gastropods primarily. The single specimen from Eniwetok had fed predominantly on hermit crabs by crushing their shells with the heavy pharyngeal teeth. It apparently forages rather widely, over and in corals and on sandy and rubble bottoms.

Species: *Coris angulata* (wrasse)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length 265 mm
Digestive tract: Mouth small, 1 pair of canines at symphyses of jaws, pharyngeal teeth heavy, molariform; stomach indistinct; intestine rather short

The alimentary tract of the single specimen examined was filled with crushed, sand-dwelling pelecypods and gastropods. This solitary wrasse is common around living coral on all reefs in water 4-20 ft deep. It feeds almost exclusively on sand-dwelling molluscs which it crushes with its heavy pharyngeal teeth.

Species: *Coris gaimardi* (wrasse)
Number examined: Eniwetok, 2 specimens
Sex: Undeveloped

Standard length: 150-250 mm
Digestive tract: Similar to *C. angulata*

Both specimens examined contained shrimps and small crushed clams and gastropods. The following items were found in addition in at least one of the specimens: isopods, foraminiferans, and polychaetes. This wrasse is uncommon in all areas visited, but is found on all types of reefs around coral patches to depths of 20 ft or more. Clams and gastropods form the bulk of its diet. It is a carnivore which forages on open sandy bottoms, although it stays near coral mounds or rock rubble.

Species: *Hemigymnus melapterus* (wrasse)
Number examined: Eniwetok, 3 specimens
Sex: Female and undeveloped
Standard length: 120-220 mm
Digestive tract: Mouth small, 1 pair of canines at symphyses of jaws, pharyngeal teeth heavy, molariform; stomach indistinct; intestine rather short

All of the specimens examined contained small crushed gastropods. The remaining food items found in lesser quantities were: Crustacea—Tanaiid isopods, Shrimp fragments, Amphipods, Crab fragments, Copepods; Foraminifera—*Calcarina* sp., undet. spp.; Algae—small, green filaments and coralline algal filaments bitten and scraped with considerable calcareous powder. This solitary wrasse, common on all reefs in depths from 4-20 ft around coral heads, is comparatively large. Its food includes both inhabitants of living coral heads and the benthonic fauna on sandy bottoms adjacent to luxuriant coral patches. It is quite possible that the algae found in two of the three specimens had been taken inadvertently.

Family Summary

The wrasses are as typical of coral reefs as the corals themselves. While most species are comparatively small, some (*Cheilinus undulatus*) reach gigantic proportions and constitute some of the largest fish ever seen on reefs. They are mostly brilliantly colored in striking contrast to the luxuriant coral patches over and in which many live. Because of their great abundance and widespread distribution on all reef types, they constitute one of the most important groups of fishes in the food complex. Several species are more typical of reef rubble and compacted sandy bottoms than they are of living coral patches.

Most of the species feed on benthonic invertebrates, particularly those on compacted sandy and rubble bottoms. A generic segregation based on food and feeding habits is not feasible. All have well-developed pharyngeal teeth adapted for crushing action. They habitually take hard-bodied species of clams, gastropods, hermit crabs, brachyurous crabs, sea urchins, heart urchins, and brittlestars, all of which are crushed before entering the stomach.

Two species examined habitually probe living ramose coral heads (*Gomphosus varius* and *Epibulus insidiator*) for the small crustaceans and polychaetes secluded in the interstices. Both have structural modifications to facilitate this mode of foraging; *G. varius* has an elongate, tubular snout, and *E. insidiator* has a highly protractile, tubular buccal apparatus. Both species had eaten invertebrates which could only have been removed from the branching corals with some such mechanism.

The availability of particular types of food had a great influence on some species which were not particularly selective in food items consumed. At Arno Atoll *Pseudocheilinus hexataenia* and *Halichoeres hoeveni* had selectively fed on the foraminiferan, *Calcarina* sp., their

stomachs and guts being completely crammed with the partly digested protozoans. However, at Eniwetok where *Calcarina* sp. is not nearly so abundant, these species had consumed mostly crustaceans.

Two species examined appear to be rather selective in that they depart from the more usual mode of benthonic foraging among the wrasses and confine their food-getting to mid-water plankters such as mysids, shrimp zoeae, crab zoeae, copepods, etc., so abundant over the reefs in areas of quiet water. These species, *T. hardwickei* and *T. lucasanum marnae*, have no special plankton feeding mechanism, so must capture each plankter individually on sight.

One species, *L. dimidiatus*, has such a unique method of feeding by "tending" other larger fish and removing the parasitic Copepoda that a detailed account of the process was described under the species account. It is the only wrasse with a considerably modified feeding apparatus. Almost all of them conform to the role of small carnivore on invertebrates inhabiting living coral and the sandy bottoms of the reefs.

Family Scaridae

Species: *Cryptotomus spinidens* (parrot fish)

Number examined: Arno, 1 specimen

Sex: Undeveloped

Standard length: 85 mm

Digestive tract: Mouth moderate in size, teeth not fully united to form a smooth beak; no stomach; intestine long, thin-walled

The single specimen examined contained algal filaments which had been grazed along with a large amount of calcareous powder, and coral polyps admixed with coral skeletal fragments. This solitary parrot fish is rather uncommon on the reefs visited, but occurs around coral mounds and coral patches in quiet lagoon waters from 6-8 feet in depth. Its feeding habits are similar to other parrot fishes which scrape reef rock for algae and living coral heads for the polyps. In this particular case much more algae is consumed than are coral polyps, hence the species is designated a grazing herbivore.

Species: *Scarus bicolor* (parrot fish)

Number examined: Eniwetok, 1 specimen

Sex: Female

Standard length: 265 mm

Digestive tract: Similar to *C. spinidens* except that the teeth are fused into a smooth beak.

The single specimen examined contained both coral polyps and algae admixed with great amounts of calcareous powder and coral skeletal fragments. This is a large, solitary parrot fish commonly seen in the surge channels and just off the edge of the ocean reef front in leeward areas of the atolls. Its food seems to consist more of coral polyps than of algae, hence it is here designated as a grazing omnivore.

Species: *Scarus sordidus* (parrot fish)

Number examined: Arno, 16; Eniwetok, 2 specimens

Sex: Females

Standard length: 61-111 mm

Digestive tract: Similar to *S. bicolor*

Food item

Percentage of fish containing the item

Coelenterata	
Coral polyps, with much skeletal material admixed	83
Algae	
Fine filaments, admixed with calcareous powder	27

This very common parrot fish forms large schools on all reefs visited in 3-20 ft of water. It is always associated with living coral patches. Scraping living coral

heads seems to be its predominant mode of feeding, although it does take some algal material. It is here designated as a grazing omnivore.

Species: Seven unidentified species of *Scarus*

Specimens examined: Arno, 6; Bikini, 2; Eniwetok, 9 specimens

Sex: Males and females

Standard length: 43-325 mm

Digestive tract: Similar to *S. bicolor*

Eleven specimens of this group had consumed coral polyps admixed with a large amount of skeletal particles, and eight specimens contained in addition algal filaments admixed with a great amount of calcareous powder. These parrot fish may therefore be designated as omnivores, with coral polyp scraping practiced somewhat more frequently than rock scraping for algal filaments.

Family Summary

Unfortunately, the taxonomic treatment of the Scaridae of the Marshall Islands, now in process at the U. S. National Museum, has not appeared in print at this writing, and, except for a few easily recognized species, too much confusion in the literature extant prevents us from making unqualified identifications of the seven species lumped in this report. Our treatment of the group should not be construed to mean that all species are similar in habitat, behavior, or influence in the coral reef community.

All parrot fish examined had scraped coral polyps, mostly from the massive, glomerate corals, particularly members of the coral genera *Porites*, *Astreopora*, and *Montipora*. The beak marks on these heads, and on the rather smooth, algal covered reef rock, are very striking, and their quantity provides a rough measure of the carrying capacity of the particular reef area. Boulenger (1922) stated that parrot fishes fed mostly on vegetable matter, corals, and hard-shelled molluses, crushing the latter with their unusual dentition. We have not found them taking molluses in the Marshall Islands. In Japan, where suitable corals are absent, the parrot fish, *Leptoscarus japonicus*, takes only algae (Suyehiro 1942).

Parrot fish are very common inhabitants of all reef areas with living coral. Most species travel in small schools, although a few are solitary, and others are simply gregarious. Particularly common in the back ridge trough of the seaward reef are three large species which form schools of 10 to 50 individuals. These schools are spaced at rather even intervals of a few hundred feet along the seaward reefs. These schooling species are particularly common in surge channels where they go when the water over the seaward reef becomes shallow at ebb tides.

As swimmers approach large parrot fish they usually move off over sandy bottom patches between coral mounds where, at rather frequent intervals, they are observed to void as feces great masses of calcareous powder. There is little doubt that parrot fish contribute substantially to the formation of fine sand by scraping coral and rock surfaces, digesting the algae and coral polyps, and returning the pulverized rock and skeletal material to the bottom as fecal components.

Family Gobiidae

Species: *Gnatholepis unjerensis* (goby)

Number examined: Arno, 5 specimens

Sex: Males and females

Standard length: 32-40 mm

Digestive tract: Mouth small, inferior, villiform teeth on jaws, pharyngeal teeth heavy; stomach indistinct; intestine long, coiled

Food item	Percentage of fish containing the item
Crustacea	
Copepods	100
Copepod metanauplii	20
Ostracods	20
Crustacean fragments	20
Detritus, with admixed sand grains	60
Algae	
Fine filaments, admixed with sand grains	40
Gastropoda	
Crushed small gastropods	20

This small goby is ubiquitous on all quiet, compacted sandy bottoms 3-25 ft in depth on lagoon, interisland, and seaward reefs. It is strongly demersal, lives on the sandy bottoms, and retreats into burrows or under rocks when disturbed. This species is omnivorous, taking any food available to it among the benthos. It also makes use of detritus to a certain extent. The rather heavy pharyngeal teeth enable it to crush small, thin-shelled gastropods and crustaceans.

Species: *Gobius ornatus* (goby)
Number examined: Arno, 13 specimens
Sex: Males and females
Standard length: 31-65 mm
Digestive tract: Similar to *G. anjerensis*

Food item	Percentage of fish containing the item
Crustacea	
Copepods	84
Copepod metanauplii	7
Isopods	69
Ostracods	53
Amphipods	7
Polychaeta	
Unid. polychaetes	46
Foraminifera	
Several unid. species	23
Gastropoda	
<i>Atys</i> sp.	15
Algae	
Fine filaments, with sand grains	7
Sand grains	61

This species lives in burrows in compacted sand bottoms 3-25 ft deep wherever the water is quiet. It is carnivorous, feeding almost exclusively on small benthonic species which it catches in a rather selective way, favoring crustaceans and polychaete worms.

Species: *Bathygobius fuscus fuscus* (goby)
Number examined: Arno, 14 specimens: 1 empty
Sex: Males and females
Standard length: 32-66 mm
Digestive tract: Mouth terminal, large, teeth villiform, pharyngeal teeth not heavy; stomach large, thick-walled; intestine short, 1 loop

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	30
Shrimp fragments	23
Polychaeta	
Unid. polychaetes	23
Fish	
Unid. fragments	15
Wrasse	7
Goby	7
Insecta	
Ant	15
House fly	7
Algae	
Fine filaments, admixed with sand grains	7

This species is exceedingly abundant, particularly in the intertidal zone on all reefs. It is an ubiquitous inhabitant of the tide pools and shallow depressions. When pursued it leaps from pool to pool, apparently exhibiting a thorough "memory" of its immediate sur-

roundings, since the leaps from pool to pool are accurate and rapid. In addition, it has definite homing tendencies. The fused ventral fins make an effective sucking disc with which it can cling to rock surfaces as the waves surge over it. Its food and feeding characteristics, combined with its digestive morphology, label the species as a carnivore, feeding mostly on the benthonic fauna of tidal flats and the inhabitants of tide pools. Occasionally it will scrape off some algal filaments.

Species: *Gobiodon erythrosipilus* (goby)
Number examined: Arno, 5 specimens: 1 empty
Sex: Males and females
Standard length: 28-31 mm
Digestive tract: Mouth terminal, small; teeth villiform with some canines on inner row of lower jaw, 2 pairs rather strong near the symphysis; stomach large, heavy-walled; intestine short

Two of the four specimens examined contained only fish eggs, one of the others contained only isopods, and the fourth had a polychaete worm. This goby lives exclusively in the interstices of living heads of ramose corals (*Pocillopora* sp., *Acropora* sp., *Stylophora* sp.), and thus is found commonly on all quiet reefs where these corals occur in shallow water. Each head seems to have 1-10 individuals within it. They will not leave the coral head, even after it has been taken from the water. The heavy diet of fish eggs resulted from our sampling during the time when several species of coral-inhabiting fish were spawning. Since several of these fish spawn in the interstices of living corals, it is not unusual for the eggs to be eaten by such carnivorous coral-dwelling inhabitants. They also take small crustaceans and polychaetes which inhabit living corals.

Species: *Gobiodon rivulatus* (goby)
Number examined: Arno, 11 specimens: 3 empty
Sex: Males and females
Standard length: 21-33 mm
Digestive tract: Similar to *G. erythrosipilus*

Food item	Percentage of fish containing the item
Crustacea	
Copepods	50
Copepod metanauplii	25
Isopods	25
Polychaeta	
Unid. polychaetes	25
Detritus and fine sand grains	12

This species occupies the same habitat in the same reef areas as does *G. erythrosipilus*. Frequently, a single coral head will contain both species. As a matter of fact, it is entirely possible that what we identified as *G. rivulatus* may be a mixture of two closely-related species, *G. rivulatus* and *G. quinquestrigatus* (Cuvier and Valenciennes). In any event, they appear to have very similar carnivorous food predilections, taking small inhabitants of the coral heads in which they live. The detritus and fine sand found in one specimen examined probably was taken in as the fish was succumbing to rotenone poisoning.

Species: *Paragobiodon echinocephalus* (goby)
Number examined: Arno, 8 specimens: 5 empty
Sex: Females
Standard length: 12-19 mm
Digestive tract: Similar to *G. erythrosipilus* except that both

jaws have well-developed canines, and gravid females appeared to have no intestine at all, although it may have been collapsed and enclosed by the distended ovaries.

One of the three specimens with food had shrimp fragments, the other two contained isopods. These minute, highly carnivorous ramose coral-dwelling gobies, occur on all reefs with quiet water and luxuriant coral

growth, each head containing 1-10 individuals. The habits of this species are essentially similar to *G. erythrosipilus*. Here again there is a complex of very similar forms, other species found in identical habitats being *P. kerri* and *P. melanostomus*. Appearance, habitat, and behavior were very similar for all three forms. The gravid females examined contained no food, nor could we locate any digestive tract. It is possible that it could have been overlooked, should it have been entwined among the ovaries.

Family Summary

Usually solitary, sometimes in pairs, at other times in gregarious aggregations, gobies live in ramose corals, as commensals in burrows made by fossorial shrimps or other forms, or on bottoms of tidepools, tidal flats, or shallow lagoon sandy-bottomed areas. For the most part they are carnivorous, but some are actually omnivorous, taking a considerable amount of fine algal filaments and detritus along with small prey species.

From the standpoint of habitats occupied, and to a lesser extent the type of food items consumed, gobies can be segregated into two groups; those which live exclusively in living ramose coral heads, and those living elsewhere.

The most important tidepool and seaward reef flat inhabitant is *B. f. fuscus*, and in burrows on compacted sandy bottoms are found *G. ornatus* and *G. anjerensis*. The food of these species is predominantly small crustaceans and polychaetes, but *G. anjerensis* consumes far more algae and detritus than any of the others and can be designated an omnivore.

In living, ramose corals, particularly in *Pocillopora*, *Stylophora*, and *Acropora* heads, are the minute carnivorous species *G. rivulatus*, *G. erythrosipilus*, and *P. echinocephalus*. Their food consists of the neighboring small invertebrates occupying the same coral head.

Suyehiro (1942) reporting on the food and feeding habits of several gobies in Japan, also indicated heterogeneous feeding habits for the various species, accompanied by changes in the nature of the digestive tract. He also showed that the food habits of one species, *Chasmichthys gulosus*, changed markedly during growth, from microplankton as juveniles to copepods as they grew slightly larger, and, as adults, to eating each other mostly, but varying the diet with isopods, amphipods, and nereid worms. Other species were zooplankton feeders (*Pterogobius elapoides elapoides*), diatom feeders (*Boleophthalmus pectinirostris*), and scavengers (*Periophthalmus cantonensis*).

Family Eleotridae

Species: *Valenciennaea violifera* (sleeper)

Number examined: Arno, 13; Eniwetok, 5 specimens

Sex: Males and females

Standard length: 40-85 mm

Digestive tract: Mouth large, canine teeth strong in front of both upper and lower jaws, pharyngeal teeth weak; stomach indistinct; intestine long, coiled.

Food item

Percentage of fish containing the item

Crustacea	
Copepods	100
Cypris larvae	11
Ostracods	88
Isopods	83
Amphipods	16
Shrimp fragments	5
Gastropoda	
<i>Aplysia</i> sp.	33
Unid. small gastropods	5
Foraminifera, several species	27

Polychaeta	
Unid. polychaetes	16
Pelecypoda	
Small clams	5
Sand grains	72

This sleeper occurs in pairs which live in permanent burrows in compacted sandy bottoms usually beneath a rock. It plugs its burrow with a ball of algae. It is common on all compacted sandy bottoms in depths up to 15 ft on the lagoon, interisland, and seaward reefs where the water is quiet.

The very long intestine suggests that this species ought to subsist to a considerable extent on detritus, but our results indicate that it is, instead, a carnivorous species which subsists on benthonic invertebrates without being particularly selective among them. Crustaceans form the bulk of its diet, but they also comprise the most abundant benthic group. The fish can be observed to take in a mouthful of the surface material, sift it, and reject the unwanted portion through the gills while swallowing the remainder.

Species: *Valenciennaea striata* (sleeper)

Number examined: Arno, 9; Eniwetok, 11 specimens: 2 empty

Sex: Males and females

Standard length: 44-116 mm

Digestive tract: Similar to *V. violifera*

Food item	Percentage of fish containing the item
Crustacea	
Cyclopoid copepods	66
Harpacticoid copepods	11
Calanoid copepods	5
Copepod metanauplii	11
Ostracods	66
Unid. isopods	50
Tanaid. isopods	5
Cypris larvae	33
Shrimps	5
Mollusca	
Small gastropods and veliger larvae	33
Pelecypoda	
Small clams	5
Echinodermata	
Small echinoids	11
Fish	
Unid. fragments	5
Fish eggs	5
Sand grains	50

The habitat and behavior of this common sleeper is essentially the same as that for *V. violifera*. Both species may be found in the same sandy area. Its food habits are exceedingly heterogeneous, and its diet appears to be those items met as the fish scans the benthos and sifts it for food.

Family Summary

Both species of sleepers examined appear to have virtually identical habits and distribution on the sandy-bottom reefs in quiet water. The sandy bottoms occupied are those in which some rocky rubble is present under which they construct their permanent burrows. In so doing they carry out the sand in their mouths and eject it at the entrance to the burrow. They are rather busy fish, and when not sifting the benthos for food, seem to be engaged in lengthening their burrows. When they retreat into the burrow they pull a ball of algal filaments into its opening to plug the hole. This activity was observed many times on the lagoon reef at Arno in water 2-30 ft deep.

They forage by taking in a mouthful of sand and benthos, apparently sift it, then eject the unwanted portion through the gills. They are certainly not selective feeders, but some species taken must be captured on

sight, rather than sifted from the benthonic surface layer. The items taken from sifted sand appear in about the same proportion as they occur naturally in the benthos.

Family Microdesmidae

Species: *Paragobiodoides grandoculis*

Number examined: Eniwetok, 4 specimens: 2 empty

Sex: Females

Standard length: 88-90 mm

Digestive tract: Mouth large, canines well-developed in rows on both jaws; intestine short.

The two specimens examined had taken a small portunid crab and a larval shrimp. This unusual, elongate fish hovers solitarily over the light sand on lagoon reefs at depths of 6-20 ft or more, where it can be detected only by close inspection because of its slenderness and pale coloration. It remains just a few inches above the substrate, rather motionless, but when approached by a swimmer it dives into a burrow. Whether the burrows are self-constructed or are polychaete tubes was not determined. In laboratory aquaria the species readily entered "burrows" made from glass tubing. This microdesmid is a carnivore, taking small crustaceans from the benthos. The well-developed canines and large mouth provide it with an efficient mechanism for catching small prey species.

Family Echeneidae

Species: *Echeneis naucrates* (Pilot fish, shark-sucker)

Number examined: Eniwetok, 1 specimen: empty

Sex: Undeveloped

Standard length: 660 mm

Digestive tract: Mouth large, small, sharp teeth on jaws; stomach and intestine a single broad, straight tube.

The specimen examined contained garbage only, and was one of several remoras frequenting the garbage dump at Eniwetok. Several were observed attached by the elliptical sucker on the dorsal side of the head, to sharks (*Ginglymostoma*, *C. melanopterus* and *C. menisorrah*) and to a large grouper, *Promicrops lanceolatus*. Frequently it has been suggested that these fish feed on fragments of food which the larger, host fishes drop while they themselves are feeding. Both Jordan (1907) and Boulenger (1922) state that these fish are carnivores, and Suyehiro (1942) examined three specimens, all of which were empty. Recently (Maul 1956) various echeneids have been shown to feed upon ectoparasites presumably removed from the skin of their hosts.

Family Parapercidae

Species: *Parapercis cephalopunctata* (sand perch)

Number examined: Arno, 19; Bikini, 2; Eniwetok, 4 specimens: 1 empty

Sex: Males and females

Standard length: 70-121 mm

Digestive tract: Mouth moderate in size, jaws heavily armed with recurved canines; stomach large; intestine short, straight.

Food item

Percentage of fish containing the item

Crustacea

Xanthid crabs	54
Malid crabs	8
Portunid crab fragments	8
Shrimp fragments	25
Palaeomonid shrimps	8
Stomatopod fragments	8
<i>Galathea</i> sp.	4

Fish

Unid. fragments	25
<i>Apogon novemfasciatus</i>	4
Fish eggs	4

Parapercids are common on all reefs visited where they live solitarily under coral heads adjacent to sandy bottoms, or lie motionless on the sand which they closely resemble in pattern and color. This species is a voracious, demersal carnivore which lies in wait for its prey, then, when it is sufficiently close, makes a rapid dash of one or two feet along the bottom or into mid-water to make the capture. Both crustaceans and fish are taken as available.

Species: *Parapercis clathrata* (sand perch)

Number examined: Arno, 2 specimens

Sex: Females

Standard length: 122-126 mm

Digestive tract: Similar to *P. cephalopunctatus*

One of the specimens examined contained shrimp fragments; the other had consumed a portunid crab. This species is uncommon on the reefs visited, but it occupies the same habitat and has a behavior pattern similar to that described for *P. cephalopunctatus*.

Family Summary

Sand perch are solitary fish which lie on exposed sandy bottoms, on rocky surfaces, or just beneath coral heads. Their coloration obliterates them effectively as they lie motionless on the sandy substrate. Because of this feature they feed by lying in wait for crustaceans and small fish to come close to them. They seize their prey with a rapid dart of at most 2-3 ft. Their rather large mouths and recurved canines, together with their feeding methods, are much like those of lizard fish (Synodontidae), except that the dentition of sand perch is somewhat less-developed and they are more sluggish.

Family Blenniidae

Species: *Aspidontus taeniatus* (blenny)

Number examined: Arno, 3 specimens

Sex: Males and females

Standard length: 82-92 mm

Digestive tract: Mouth small, minute teeth on both jaws and 1 pair of enormous, recurved fangs on lower jaw; intestine short.

One of the fish examined contained shrimp fragments, another had consumed fish eggs, and the third contained only gurry in its stomach. The color and color pattern of this brilliantly hued blenny are exceedingly like that of the wrasse, *Labroides dimidiatus*, discussed earlier. It is uncommon, but seen occasionally on the seaward and interisland reefs about living coral patches in depths from 3-6 ft and on the lagoon reef around coral mounds down to a depth of about 20 ft. It frequently lives in pipes, tubes, etc., and usually occurs in pairs. It is one of the few fish which will bite severely if handled. This species is carnivorous, taking small crustaceans and fish, usually from living coral heads. Doty & Morrison (1954) apparently mistook this blenny for *L. dimidiatus* in their description of the blenny's behavior as regards its foraging for parasites on the bodies of parrot fish. The almost perfect mimicry, possibly on the part of this blenny (Randall 1955), would make such mistaken identity easily possible.

Species: *Istiblennius coronatus* (blenny)

Number examined: Bikini, 2; Eniwetok, 3 specimens

Sex: Males and females

Standard length: 73-85 mm

Digestive tract: Mouth large, jaws with numerous fine teeth; intestine very long, coiled.

All of the specimens examined had taken large amounts of detritus and fine sand with many algal filaments admixed. Two specimens also contained the fora-

miniferan, *Calcarina* sp. This blenny is abundant on the seaward reef flats in the intertidal zone. It occurs only on hard bottoms where it lies with just its head protruding from holes and crevices. It is extremely active and alert. During feeding it apparently scoops up the surface sediments on the hard substrate which consist of fine sand, detritus, fine algal filaments and the organic leptopel which covers the substrate in most reef and shore areas (Strasburg Ph.D. thesis).

Species: *Istiblennius paulus* (blenny)

Number examined: Arno, 19; Bikini, 3 specimens: 1 empty
Sex: Males and females
Standard length: 51-130 mm

Digestive tract: Similar to *I. coronatus*.

Food item	Percentage of fish containing the item
Detritus and fine sand grains	71
Algae	
Fine filaments, with fine sand	61
Scraped filaments, with fine sand	28
Diatoms	38
Foraminifera	
<i>Calcarina</i> sp.	38
Unid. species	33
Crustacea	
Ostracods	28
Copepods	28
Gastropoda	
Unid. minute gastropods	4

This very abundant species occurs on all hard-bottomed reef shallows. It lives on permanently submerged reef flats in depths of 1-2 ft, and not intertidally as does *I. coronatus*. It is an extremely agile and alert species. Like *I. coronatus*, *paulus* also lies on the bottom with just its head protruding from its hiding place. *I. paulus* is quite omnivorous, taking primarily detritus, leptopel, and benthonic algae and invertebrates by scraping off the thin, sedimentary layer on the reef rock or on compacted sand. It appears to ingest this benthos without exercising much selection between organisms.

Species: *Exallias brevis* (blenny)

Number examined: Bikini, 1 specimen
Sex: Female
Standard length: 80 mm
Digestive tract: Similar to *I. coronatus*

The single specimen examined contained fine, filamentous algae and detritus admixed. This uncommon species is found on both the lagoon and seaward reefs in depths from 4-15 ft near living coral. It hides below the living coral heads, the adults being very demersal; however, the young are pelagic. It is predominantly an herbivore scraping the fine algal filaments from the bases of coral heads and coral rock.

Species: *Cirripectes variolosus* (blenny)

Number examined: Bikini, 1 specimen
Sex: Female
Standard length: 70 mm
Digestive tract: Similar to *I. coronatus*

The single specimen examined had taken fine algal filaments with detritus admixed, but no sand grains. This common species occurs most abundantly on the seaward reef flat from about the middle to the outer edge, being more abundant in areas containing much living coral. Apparently it prefers regions having considerable water movement. It lives in small holes in the hard substrate, and frequently is seen swimming actively about living coral. Its food consists of fine algae and the precipitated detritus or leptopel which covers rocks in its living area.

Species: *Cirripectes sebae* (blenny)

Number examined: Arno, 9 specimens

Sex: Males and females
Standard length: 25-71 mm
Digestive tract: Similar to *I. coronatus*

Food item	Percentage of fish containing the item
Detritus	88
Algae	
Fine filaments, with fine sand grains admixed	77
Diatoms	22
Foraminifera	
<i>Calcarina</i> sp.	33
Ostracoda	
Gastropoda	
Minute gastropods	11

This abundant species prefers regions of considerable water movement and is found most commonly at the outer reef edge and in surge channels on leeward ocean reefs 3-10 ft deep. There it lives in small holes in the substrate, and is often seen flitting about living coral. It has a tendency to move about the reefs rather than to remain secluded in one hole. This species, like *C. variolosus*, subsists on the organic materials on the surface of the hard substrate, particularly on precipitated detritus and fine algal filaments. In the process of scraping off this sediment, it takes minute animal forms (ostracods, foraminiferans) which occur in the benthos.

Family Summary

These active, small fish are found in most habitats on coral reefs, but most of them prefer the seaward reefs, either on the seaward reef flat, or in surge channels and the back ridge trough.

Most species are morphologically adapted to consume a diet heavy in detritus and fine filamentous algae. With this material, gotten by scraping the sediments and organic covering of rocks or hard bottoms, they secure some minute animal species such as foraminiferans, ostracods, copepods, etc., which comprise part of the benthos. There is little question, however, that their diet must be high in leptopel, and experimental holding of several species in captivity has verified this.

Within the family, however, there are some aberrant types which have very different food and foraging habits. One of these examined, *A. taeniatus*, is strictly carnivorous, taking both crustaceans and fish, and not at all morphologically suited to a diet of detritus and algae. Suyehiro (1942) reported on the feeding habits of three genera of blennies, one of which was entirely herbivorous, and two strictly carnivorous. He remarked about the heterogeneity in digestive morphology and food habits and questioned the taxonomic parameters of the family.

Family Brotulidae

Species: *Dinematicthys iluoceteoides* (brotulid)

Number examined: Arno, 12; Bikini, 4 specimens: 4 empty
Sex: Males and females
Standard length: 34-83 mm
Digestive tract: Mouth large, canines in jaws numerous and well-developed; stomach heavy-walled; intestine short.

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	33
Crab fragments	25
Isopods	8
Ostracods	8
Fish	
Unid. fragments	25
Gurry	8

This brotulid is uncommon, but occurs on all reefs visited. It is present at the leeward ocean reef edge and in the surge channels. In the lagoon it lives in coral

mounds in about 8-10 ft of water. It has very secretive habits, none ever having been seen alive by us, and apparently secludes itself in holes or crevices in coral. It is a voracious carnivore, taking mostly crustaceans and fish which venture close to its hiding place. From its appearance and seclusiveness we judge it to be very demersal, probably lying in wait for its prey which it dashes out to capture.

Family Balistidae

Species: *Rhinecanthus rectangulus* (trigger fish)
Number examined: Arno, 4; Bikini, 3; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 50-160 mm
Digestive tract: Mouth small, teeth heavy, incisiform, almost fused, pharyngeal teeth not heavy; stomach heavy-walled; intestine long, coiled.

Food item	Percentage of fish containing the item
Algae	
Scrapings and filaments, with much calcareous powder	75
Filaments, without sand	12
Crustacea	
Isopods	87
<i>Thalamita</i> sp.	12
Copepods	12
<i>Gonodactylus</i> sp.	12
Polychaeta	
Unid. fragments	12
Foraminifera	
<i>Calcarina</i> sp.	12

This is a very common trigger fish on the seaward reef shallows and on the interisland reefs. It never strays far from its refuge hole or crevice in the hard bottom. It characteristically forages about the shallow reefs away from living coral. The species is omnivorous, taking algae and crustacea primarily. The crustaceans taken are common residents of the sandy and rubble bottoms.

Species: *Rhinecanthus aculeatus* (trigger fish)
Number examined: Arno, 7; Bikini, 1; Eniwetok, 7 specimens
Sex: Males and females
Standard length: 105-181 mm
Digestive tract: Similar to *R. rectangulus*

Food item	Percentage of fish containing the item
Algae	
Scrapings, mixed with minute rocky fragments	93
Algal fronds, bitten off	33
Coralline algal fragments	13
Gastropoda	
<i>Alys</i> sp.	40
Small, crushed gastropods	13
Foraminifera	
<i>Calcarina</i> sp.	40
Crustacea	
Isopods	33
Crab fragments	26
Shrimp fragments	20
Amphipods	6
Polychaeta	
Unid. fragments	20
Pelecypoda	
Crushed clams	6
Fish	
Unid. fragments	13
<i>Chromis caeruleus</i>	6
Coelenterata	
<i>Acropora</i> sp., tips broken off	6

This trigger fish is common on the lagoon and inter-island reef shallows, and on the seaward reef only in areas of quiet water. It prefers a compacted sandy bottom or one with rubble near coral mounds. Such a heterogeneous feeder can only be omnivorous with no particular predilections noted. It apparently takes anything organic, whether it be soft- or hard-bodied.

Those containing *Acropora* tips had consumed great numbers of them, and the intestine was crammed with the sharp skeletal fragments.

Species: *Balistapus undulatus* (trigger fish)
Number examined: Arno, 12; Eniwetok, 8 specimens
Sex: Males and females
Standard length: 115-205 mm
Digestive tract: Similar to *R. rectangulus* except that teeth in front are much heavier and stronger

Food item	Percentage of fish containing the item
Coelenterata	
<i>Acropora</i> sp., living tips of branches	65
Scraped polyps, with much skeletal powder	10
<i>Pavona varians</i> , fragments of living corallum	5
<i>Styloster sanguineus</i> , fragments	5
Fish	
Unid. fragments	55
<i>Abudefduf biocellatus</i>	5
Crustacea	
Crab fragments	45
Xanthid crab fragments	30
Unid. hermit crab	5
Shrimp fragments	20
Gastropoda	
Crushed shells	45
Crushed vermetid tubes	10
<i>Cypraea carneola</i> , crushed	5
Algae	
Fronds, bitten off	45
Fine filaments and scrapings, with much calcareous powder	35
Coralline algal fragments	15
Echinodermata	
<i>Echinometra mathaei</i> , crushed	15
Euclidarid urchin, crushed	10
Spatangid heart urchin, crushed	5
Tunicata	
Unid. fragments	10
Pelecypoda	
Clam fragments	10
<i>Arcia</i> sp., crushed	5
<i>Chama</i> sp., crushed	5

This common trigger fish frequents all deep, quiet reefs with considerable living coral, in depths from 4-20 ft. Its omnivorous habits of a completely heterogeneous nature are evident from the table of food items consumed. Although unselective, specimens were encountered frequently which had consumed a meal entirely of one or two items. This was especially true of those that had broken off living tips of ramose corals, and those that had taken tunicates. The strong teeth are used to break off corals, and to crush gastropods, echinoderms, etc. Even coralline algae had been broken off and consumed. Eight specimens examined by Randall (1955) in the Gilbert Islands had similar food habits, even to tunicate fragments, sea urchins, and *Acropora* sp. tips.

Species: *Balistoides viridescens* (trigger fish)
Number examined: Eniwetok, 2 specimens
Sex: Males
Standard length: 490-515 mm
Digestive tract: Similar to *B. undulatus*

One specimen had consumed mostly the living tips of *Pocillopora damicornis*, but also contained crushed shells of eake urchins (*Clypeaster* sp.) and sea urchins (*Eucidaris metularia*), and crushed boring clams, *Lithophaga* sp. The other specimen had eaten solely starfish of an unidentified genus. This solitary species, though uncommon, is large and striking in shape and coloration. It occurs on lagoon reefs around living coral mounds or over sandy bottoms near living coral patches, and on the seaward reef it is found in sheltered areas near coral mounds. *B. viridescens* is strictly a carnivore, subsisting mostly on living coral and echinoderms.

Species: *Pseudobalistes flavimarginatus* (trigger fish)
 Number examined: Arno, 1; Eniwetok, 1 specimen
 Sex: Female and undeveloped
 Standard length: 190-460 mm
 Digestive tract: Similar to *B. undulatus*

The food items consumed by the two specimens examined included: Crustacea—*Lydia annulipes*, Isopods; Gastropoda—crushed *Oliva* sp., crushed unid. gastropods; Foraminifera—*Calcarina* sp.; Tunicata—colonial tunicate fragments. This uncommon, solitary trigger fish grows to about 2 ft in length. It was found on the lagoon and interisland reefs where the water was quiet and 10-30 ft deep. It appears to be entirely carnivorous and not particularly selective about its food items. Although these specimens had eaten no coral tips, it is likely that they do take them on occasion.

Species: *Pseudobalistes fuscus* (trigger fish)
 Number examined: Arno, 1 specimen
 Sex: Not noted
 Standard length: 310 mm
 Digestive tract: Similar to *B. undulatus*

This specimen contained the following food items: Echinodermata—Heart urchin fragments; Foraminifera—*Calcarina* sp., *Marginopora* sp., unid. foraminiferans; Gastropoda—Vermiid fragments; Pelecypoda—Protocerchs. This large, solitary trigger fish is uncommon, and is found swimming over sandy bottoms in water 10-20 ft in depth. It swims near the bottom, and takes refuge when molested in piles of coralline rubble or under rocks. This species appears to be entirely carnivorous, taking hard-bodied fossorial echinoderms, and breaking off vermetid tubes from their attachment to rocks.

Species: *Melichthys vidua* (trigger fish)
 Number examined: Eniwetok, 1 specimen
 Sex: Female
 Standard length: 140 mm
 Digestive tract: Similar to *B. undulatus*

The single specimen of this species contained the following food items: Algae—bitten and scraped filaments and fronds, with many sand grains and much calcareous powder; Crustacea—Xanthid crab fragments, Copepods; Pelecypoda—Small clams; Gastropoda—Small gastropods. This uncommon, solitary species is found on leeward ocean reef shallows with abundant living coral. There it hovers around living coral heads, and hides under the coral when molested. This trigger fish feeds mostly on algae, with the other animal food items being only incidental from a quantitative standpoint. It may be designated as a grazing herbivore and facultative omnivore.

Family Summary

Trigger fish, in general, adhere to a rather heterogeneous and omnivorous diet. Only the genera *Pseudobalistes* and *Balistoides* were found to be completely carnivorous, and this finding may only be the result of too few being examined. Both *P. flavimarginatus* and *P. fuscus* forage mostly on sandy bottoms taking both benthonic and fossorial forms such as echinoderms, foraminiferans, molluses, and crustaceans which they crush with their exceedingly strong teeth. *B. viridecens* varies this type of diet with meals of the living tips of ramose and cespitose corals such as *Acropora* and *Pocillopora*.

The other trigger fish examined fed on a great variety of items. One species, *B. undulatus*, apparently takes almost anything organic, soft or hard. In all these species algae comprise a prominent part of the diet,

and the intestine is very long in compensation. Admixed with the large amounts of grazed algae are fragments of the living tips of branching corals, crustaceans, fish, and molluses. Almost all of the hard-bodied organisms had been crushed into small pieces, illustrating the versatility of these fish in making a living on a coral reef.

Especially noteworthy is the fact that these trigger fish make good use of the abundant coral and even the echinoderms, the latter a group of ubiquitous organisms avoided by most predaceous animals, and for a time, thought likely to be rather well removed from the more intricate composition of the food web in coral reef communities.

Family Monacanthidae

Species: *Amanses carolae* (file fish)
 Number examined: Arno, 2 specimens
 Sex: Male and undeveloped
 Standard length: 131-151 mm
 Digestive tract: Mouth small, teeth long, heavy, incisiform; intestine long, coiled

One of the two specimens examined had the stomach and gut crammed solely with living tips of *Acropora* sp. which were partly digested. The remaining specimen had mostly fragments of a sponge (Calcispongiae), along with algal filaments and fronds bitten off, coralline algal fragments, and scraped coral polyps admixed with much skeletal material. These uncommon file fish occur on quiet, leeward ocean reefs near the outer edge, where they swim slowly about the luxuriant growth of corals and hide under them when molested. This species is omnivorous, but apparently makes a complete meal of a single item if available in sufficient quantity.

Species: *Oxymonacanthus longirostris* (file fish)
 Number examined: Eniwetok, 2 specimens
 Sex: Male and female
 Standard length: 75 mm.
 Digestive tract: Snout very long, pointed, mouth terminal, teeth protrude well beyond lips as long cupped incisors; intestine long, coiled.

Both specimens examined contained only coral polyps bitten off, with no skeletal material admixed. This small file fish is common on the lagoon, interisland, and seaward reefs where luxuriant coral growth occurs. It has been observed to have a very close association with living coral, and large numbers of them have been seen head down in living coral heads. Apparently they are engaged in nibbling off the coral polyps, a feeding method for which their dentition is well adapted. This species can be classed as strictly a carnivore.

Species: *Monacanthus* sp. (file fish)
 Number examined: Bikini, 1 specimen
 Sex: Male
 Standard length: 290 mm
 Digestive tract: Similar to *A. carolae*, but with incisors even more strongly developed.

This specimen had the entire digestive tract crammed full of the living tips of ramose and cespitose corals (*Acropora*, *Pocillopora*). Some coralline algal fragments were admixed. The fragments of coral were large, some over 1 inch in length. The intestine, being very thin-walled, protruded outward in all directions as a result of the long coral fragments contained within it. This species is probably exclusively a carnivore, although on occasion some algae may be taken.

Family Summary

All file fish examined fed almost exclusively on coral, although their feeding methods varied considerably. *O. longirostris*, for example, nibbles off the tips of expanded

polyps without touching the corallite. On the other hand, the large file fish, *Amanes carolae*, and *Monacanthus* sp., break off the ends of the branches of such ramosc and cespitose species as *Acropora*, *Pocillopora*, and *Stylophora*, and fill the entire gut with these large, sharp fragments so that the organic material may be digested. Many fragments an inch or more in length were removed from intestines having a diameter of only half that. *A. carolae* varies its diet by taking sponges and algae in addition to coral. There is little question that file fishes derive the bulk of their nutriment from living corals, and thus are important in helping to bring into circulation within the food web the abundant corals which serve comparatively few predators in relation to the vast bulk of protoplasm they represent.

Family Ostracionidae

Species: *Ostracion cubicus* (trunk fish)
Number examined: Eniwetok, 6 specimens
Sex: Males and females
Standard length: 125-260 mm
Digestive tract: Mouth small, teeth moderate, slightly incisiform; intestine very long, coiled.

Food item	Percentage of fish containing the item
Algae	
Fine algal scrapings, with calcareous powder	50
Filaments, bitten off	16
Polychaeta	
Unid. polychaetes (sand-dwelling)	50
Gastropods	
<i>Atys</i> sp.	33
Pelecypoda	
Crushed clams	16
Fish	
Unid. fragments	16
Crustacea	
Isopods	16
Xanthid crab fragments	16
Sand grains and foraminiferans	67

Trunk fish commonly inhabit all reefs where the water is relatively quiet at depths of 3-20 ft. They are very weak swimmers, cruising slowly around coral heads, hiding in caves, crevices, etc. They are completely omnivorous, taking what food items they can get, mostly from the sandy bottoms around coral mounds. Except for the algae which was probably growing on the coral mound or rocks, all food items are benthonic. The polychaetes taken are exceedingly abundant in the sandy bottoms of the lagoon just below the surface. As would be expected from its structural design and small mouth, trunk fish food getting proclivities are restricted to sedentary or slow-moving invertebrates.

Family Tetraodontidae

Species: *Arothron mappa* (puffer, balloon fish)
Number examined: Arno, 2 specimens
Sex: Male and female
Standard length: 405-540 mm
Digestive tract: Mouth moderately small, teeth 2 large plates in each jaw forming a beak; intestine very long, coiled.

Both specimens examined had the entire digestive tract distended with large fragments of a sponge. In addition a few other food items listed below had been taken: Tunicata fragments; Gastropoda—Crushed shells; Crustacea—Xanthid crab fragments; Algae—Coralline algal fragments, *Halimeda* branches, *Valonia* sp. This large, reticulated puffer is uncommon, occurring in our collections only from the lagoon reef shallows of Arno Atoll. It apparently stays near the lagoon reef edge in 5-10 ft of water. Its noteworthy feeding on sponges is significant in bringing another, little preyed upon organism into the food web.

Species: *Arothron hispidus* (puffer, balloon fish)
Number examined: Arno, 1 specimen
Sex: Male
Standard length: 300 mm
Digestive tract: Similar to *A. mappa*

The single specimen examined contained the following items in its stomach: Pelecypoda—*Pinctada martensi* (crushed), *Codakia punctata* (crushed), *Valsella auriculata* (crushed), *Isognomon costellatum* (crushed); Coelenterata—fine tips of *Pocillopora damicornis*; Porifera fragments; Tunicata fragments; Crustacea—Xanthid crab fragments; Algae—Coralline algal fragments, *Halimeda* fragments. This puffer is uncommon in the Marshall Islands and occurs mostly in the quiet water of the lagoon near living coral at depths of 4-20 ft. It usually secludes itself under a ledge or in a hole in the coral. This species is omnivorous, though primarily a carnivore. The heterogeneity of food habits indicates that it is an opportunist, taking whatever animal food it can get at the time. Its heavy teeth are well adapted for crushing hard-bodied forms and breaking off branches of living coral.

Species: *Arothron meleagris* (puffer, balloon fish)
Number examined: Arno, 3 specimens
Sex: Females
Standard length: 158-176 mm
Digestive tract: Similar to *A. mappa*

In the Marshall Islands this species is almost exclusively a feeder on live coral. All specimens examined contained many living tips of *Acropora* sp., and the following species of corals were taken by at least one of the specimens examined: *Porites lobata* fragments, *Porites superfusa* fragments, *Goniastrea parvistella* fragments, *Pavona varians* fragments, *Montipora* sp. fragments, Aleyonarian tips. The entire gut in all three specimens was choked with the stony fragments of several species of living coral. This puffer is uncommon in the Marshall Islands, and in our collections was taken only at Arno Atoll. There it frequents lagoon reefs wherever luxuriant growths of coral occur. It secludes itself in holes or crevices, or under the living coral heads.

Species: *Arothron nigropunctatus* (puffer, balloon fish)
Number examined: Arno, 1; Eniwetok, 4 specimens
Sex: Females and undeveloped
Standard length: 120-158 mm
Digestive tract: Similar to *A. mappa*

Except for crab fragments in one specimen and unidentified crushed clams in another, these puffers had eaten only living tips of *Acropora* sp. The stomach and intestine of each specimen were completely crammed with the stony branches, those in the stomach just beginning to undergo digestion, while those in the lower intestine were white and cleaned of the fleshy polyps. This puffer is the most common one in the Marshall Islands where it occurs on all reefs having living coral from 2-20 ft deep. Although it is predominantly a carnivore taking living coral as food, it can and does, on occasion, take other organisms such as crustaceans and molluses. Randall (1955) examined two specimens in the Gilbert Islands and found them both to contain nothing but bite-sized pieces of living coral.

Species: *Arothron* sp. (puffer, balloon fish)
Number examined: Eniwetok, 4 specimens: 3 empty
Sex: Males and females
Standard length: 420-600 mm
Digestive tract: Similar to *A. mappa*, but with more highly developed upper pharyngeal teeth

The single specimen with food contained nothing but ossicles of the recently digested sea star, *Linckia guildingii*. This puffer, taken off the pier at Eniwetok, was not seen elsewhere by us. It is a very large species, attaining a length of over 2 ft.

Family Summary

The puffers, like the trigger fish, have interesting food habits because they incorporate into the food web so many kinds of food organisms which would not otherwise contribute to higher trophic levels because they are usually avoided as food items by other predators. In our experience no two specimens of the same species of puffer had eaten exactly the same food items, or in the same proportionate quantities. They appear to feed predominantly as opportunists, and virtually nothing alive on the reefs is beyond their capacity for utilization.

Perhaps the most consistently taken food item was living tips of ramosc and cespitose corals, and even fragments of glomerate and foliacous types which require considerable strength to break off from the remaining corallum. One specimen had eaten seven different species of corals. However, living tips of the rather delicate *Acropora* sp. heads seem to be preferred. This genus is the most abundant of the corals, and probably the easiest to break off from the main corallum. Various molluscs, particularly pelecypods growing attached to rocks and dead coral bases, are broken away from their attachment and crushed by the heavy dental armature.

Two specimens examined are especially noteworthy for having fed so extensively on unusual items. In one case, the two specimens of *A. mappa* examined from Arno Atoll, the entire gut was greatly distended, literally bloated with large chunks of sponge. Obviously, this was not a case of the chance taking of an unusual food item by them, because the two puffers were caught on different days on different parts of the reef. In another species of puffer from Eniwetok, yet unnamed, the entire gut was choked with small specimens of the ubiquitous sea star of rocky reefs and coral bases, *Linckia guildingii*.

Family Canthigasteridae

Species: *Canthigaster solandri* (sharp-backed puffer)

Number examined: Bikini, 5; Eniwetok, 11 specimens

Sex: Males and females

Standard length: 38-160 mm

Digestive tract: Mouth small, snout somewhat produced, teeth 2 large plates in each jaw forming a powerful beak; intestine long, coiled.

Food item

Percentage of fish containing the item

Algae

Fronds and scraped filaments, with much calcareous powder

81

Crustacea

Unid. fragments

12

Isopods

6

Tunicata fragments

12

Fish

Unid. fragments

6

Polychaeta

Serpulid polychaete

6

Unid. fragments

6

Foraminifera

Calcarina sp.

6

Coolenterata

Bitten off and scraped living tips of *Acropora* sp.

6

Bitten off lobes of alcyonarian coral

6

This sharp-backed puffer is very common, and locally abundant, on Marshallese reefs in all areas around living coral. It is common on the seaward reef shallows in all protected areas. The predominant food taken by these specimens was algae, but the animal composition is sufficient to designate the species as an omnivore. The dentition is especially fitted for scraping algal filaments off rocks and dead coral bases.

Family Diodontidae

Species: *Diodon hystrix* (spiny puffer)

Number examined: Arno, 1 specimen

Sex: Undeveloped

Standard length: 320 mm

Digestive tract: Mouth small, teeth in each jaw fused into 1 unit forming a powerful beak; intestine medium long.

The single specimen examined contained the following items: Gastropoda—Crushed shells; Crustacea—Xanthid crab fragments; Foraminifera—*Calcarina* sp.; coarse sand grains. The spiny puffer is rather uncommon on all reefs in the Marshall Islands and occurs where the water is relatively quiet in depths of about 8 ft. It feeds primarily on hard-shelled molluscs and crustaceans which it crushes easily with its heavy teeth and strong jaws. It is strictly a carnivore.

ANALYSIS OF FEEDING HABITS BY FORAGING METHODS

ALGAL FEEDERS

Of evolutionary significance is the fact that the herbivorous feeding habit and associated morphological and physiological changes do not appear in the more primitive fishes considered here, but make their entry with the percomorphs in the Family Mugilidae. This is not surprising, of course, because of the rise of modern bony fishes from highly carnivorous predecessors. Although our evolutionary time scales are somewhat unreliable in dating the rise of the several orders of the Osteichthyes, it is certain that these fishes were prevented from direct utilization of the tremendous plant food resources of the sea for a very long time.

The algal feeders can best be segregated into four categories, depending upon the nature of their algal foraging habits. First, there are a few which subsist to a very large extent, at least, on unicellular algal types. The mullets (Mugilidae) and some blennies (Blenniidae) are significant in this regard. Second, there are grazers on algae which crop very closely to the substrate, taking, more often than not, some of the substrate along with the algae. Here, of course, some of the surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), gobies (Gobiidae), blennies (Blenniidae), and trigger fish (Balistidae), are important. Third there are browsers which have cutting teeth for biting off bits of fronds or filaments above the substrate. In this category are placed some surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), and trigger fish (Balistidae). The fourth category includes those fishes which take algal food incidental to other food types which predominate in the diet. Some of the more important members of this group are the butterfly fish (Chaetodontidae), wrasses (Labridae), parrot fish (Scaridae), gobies (Gobiidae), and puffers (Tetraodontidae).

In the following lists the more important species in each category of algal feeding type are indicated:

Unicellular Algae

Family Mugilidae (mullet)—*N. chaptali*, *C. crenilabris*; Family Blenniidae—*I. paulus*.

Grazers

Family Leiognathidae (silver perch)—*G. argyreus*; Family Siganidae (rabbit fish)—*S. rostratus*; Family Acanthuridae (surgeon fish)—*C. striatus*, *A. olivaceus*, *A. gahm*, *A. guttatus*, *A. nigroris*, *A. xanthopterus*, *A. mata*, *Z. veliferum*, *N. lituratus*; Family Pomacentridae (damsel fish)—*P. nigricans*, *P. jenkinsi*, *P. albofasciatus*, *A. sordidus*, *A. glauca*, *A. dicki*, *A. biocellatus*, *A. amabilis*; Family Labridae (wrasses)—*H. hoenei*; Family Gobiidae (goby)—*G. anjerensis*; Family Blenniidae (blenny)—*E. brevis*, *I. coronatus*, *C. sebae*, *I. paulus*, *C. variolosus*; Family Balistidae (trigger fish)—*B. undulatus*, *R. rectangularis*, *R. aculeatus*, *M. vidua*; Family Monacanthidae (file fish)—*A. carolae*; Family Ostracionidae (trunk fish)—*O. cubicus*; Family Canthigasteridae (sharp-backed puffer)—*C. solandri*.

Browsers

Family Siganidae (rabbit fish)—*S. rostratus*; Family Kynoshidae (pilot fish)—*K. cinerascens*; Family Chaetodontidae (butterfly fish)—*C. ephippium*, *C. auriga*, *C. reticulatus*, *C. flavissimus*; Family Acanthuridae (surgeon fish)—*A. t. triostegus*, *A. achilles*, *A. guttatus*, *A. lineatus*, *A. alata*, *A. nigroris*, *Z. veliferum*, *N. unicornis*, *N. lituratus*; Family Pomacentridae (damsel fish)—*D. aruanus*, *P. vauvili*, *P. jenkinsi*, *A. saxatilis*, *A. lacrymatus*, *A. dicki*, *A. biocellatus*, *A. amabilis*, *A. septemfasciatus*; Family Balistidae (trigger fish)—*B. undulatus*, *R. aculeatus*; Family Tetraodontidae (puffers)—*A. hispidus*.

Incidental

Family Chaetodontidae (butterfly fish)—*C. vagabundus*, *C. citrinellus*; Family Pomacentridae (damsel fish)—*A. leucopomus*; Family Labridae (wrasses)—*H. melapterus*, *T. lutescens*, *H. hortulanus*, *H. marginatus*, *Stethojulis* sp., *S. axillaris*; Family Scaridae (parrot fish)—*C. spinidens*, *S. bicolor*, *S. sordidus*, Scarids (7 valid species); Family Gobiidae (goby)—*B. f. fuscus*, *G. ornatus*; Family Tetraodontidae (puffer)—*A. mappa*.

DETRITUS FEEDERS

Comparatively few species among fishes are detritus feeders. It is apparent that on coral reefs benthonic invertebrates are the chief organisms for converting the particulate and colloidal organic material in the benthonic deposits to animal protoplasm. This food source, in turn, reaches the fishes through the multitude of species which prey upon these benthonic and fossorial invertebrate forms. The following fish species depend to a very large extent upon detritus in its several physical forms for their subsistence: Family Mugilidae (mullet)—*N. chaptali*, *C. crenilabis*; Family Gobiidae (goby)—*G. anjerensis*; Family Blenniidae (blenny)—*E. brevis*, *I. coronatus*, *C. sebae*, *I. paulus*, *C. variolosus*.

SCAVENGERS

Only one species in our collections seems to fit the category of a natural scavenger, *Ginglymostoma ferugineum*, the nurse shark.

PLANKTON FEEDERS

No fish examined consumed phytoplankton, but several fed upon zooplankton, and of these only a very few have structural adaptations to facilitate sieving the minute plankters out of the water. The manta ray, *M. alfredi*, is perhaps the most highly adapted plankton feeder of the species encountered, but this species is

not actually part of the reef fauna, although it does come into the lagoons and even into comparatively shallow water on the reefs. It is believed that the cephalic fins serve to push plankters toward the wide open mouth in which peculiar organs, known as praebanchial appendages, together with the branchial apparatus, serve as straining devices as do gill rakers in other plankton-feeding fishes.

Among the more abundant small plankton feeders on the reefs are the round herring, *S. delicatulus*, the half-beaks, *H. affinis*, *H. laticeps*, and the silversides, *A. ovala* and *P. pinguis*. All of these species possess rather long, fine gill rakers for sieving out small crustacean and other plankters. One species of silversides examined, *S. temmincki*, has gill rakers only of medium length, and this species was found to feed to a great extent on the benthonic fauna rather than on mid-water plankters.

Several species of pomacentrids and two species of labrids were also found to consume plankters, but did not have special filtering devices. Rather, they selected the plankters eaten by visual means.

The following species examined subsist on zooplankton: Family Mobulidae (manta ray)—*M. alfredi*; Family Dussumieriidae (round herring)—*S. delicatulus*; Family Hemiramphidae (half-beaks)—*H. affinis*, *H. laticeps*; Family Atherinidae (silversides)—*A. ovala*, *P. pinguis*, *S. temmincki*; Family Pomacentridae (damsel fish)—*D. aruanus*, *C. caeruleus*, *C. atripectoralis*, *P. pavo*; Family Labridae (wrasses)—*T. hardwickei*, *T. lucasanum marnae*.

CARNIVORES

Coral reefs of the Marshall Islands are replete with carnivores of all sizes, and with a great variety of prey. The carnivores are segregated below into groups which predominantly, or to a great extent at least, seek their prey among the fossorial fauna, benthonic fauna, or mid-water fauna. Lastly the larger, roving carnivores are segregated into those characteristically dwelling on the reefs, and those deep or open water forms which forage over the reefs at regular or irregular intervals. In some cases carnivorous species forage rather widely and are classed in more than one of the groupings listed.

Carnivores on Fossorial Fauna

Family Ophichthidae (snake eels)—*L. semicinctus*, *B. sauropsis*; Family Moringuidae (whip eels)—*M. macrochir*; Family Holocentridae (squirrel fish)—*M. microphthalmus*, *H. diadema*; Family Polynemidae (thread fins)—*P. sexfilis*; Family Lutjanidae (snappers)—*L. gibbus*, *G. griseus*; Family Sparidae (snapper)—*M. grandoculis*; Family Mullidae (goat fish)—*M. samoensis*, *P. barberinus*; Family Labridae (wrasses)—*C. gaimardi*, *C. angulata*, *C. trilobatus*, *H. trimaculatus*, *H. hortulanus*, *H. marginatus*, *Stethojulis* sp., *S. axillaris*; Family Balistidae (trigger fish)—*B. undulatus*, *P. fuscus*; Family Ostracionidae (trunk fish)—*O. cubicus*.

Carnivores on Benthonic Fauna

Family Orectolobidae (carpet sharks)—*G. ferrugineum*; Family Clupeidae (sardines)—*H. kunzei*; Family Muraenidae (moray eels)—*E. zebra*, *E. leucotaenia*, *E. polyzona*, *G. pictus*, *G. petelli*, *G. javanicus*, *G. flavimarginatus*; Family Congridae (conger eels)—*C. noordzicki*; Family Synodontidae (lizard fish)—*S. variegatus*, *S. gracilis*; Family Bothidae (flounders)—*B. mancus*; Family Holocentridae (squirrel fish)—*M.*

berndti, *M. microphthalmus*, *H. sammaria*, *H. lacteoguttatus*, *H. microstomus*, *H. laevis*, *H. diadema*, *H. spinifer*; Family Syngnathidae (pipe fish)—*C. i. waitei*, *C. f. conspicillatus*; Family Atherinidae (silversides)—*S. temmincki*; Family Polynemidae (thread fins)—*P. sexfilis*; Family Carangidae (jacks)—*T. crumenophthalmus*; Family Apogonidae (cardinal fish)—*P. quinquecinctata*, *C. macrodon*; Family Serranidae (groupers)—*E. merra*, *E. fuscoguttatus*, *E. kohleri*, *E. hexagonatus*, *E. macropsilops*, *E. spilotus*, *V. louti*, *C. argus*, *C. urodelus*, *A. leucogrammus*, *P. truncatus*; Family Pseudochromidae—*P. melas*, *P. nigricans*; Family Leiognathidae (silver perch)—*G. argyreus*; Family Pempheridae (sweepers)—*P. oualensis*; Family Lutjanidae (snappers)—*L. monostigma*, *L. bohar*, *L. vitta*, *L. vaigiensis*, *L. gibbus*, *G. griseus*, *L. microdon*, *G. aureolineatus*; Family Sparidae (snappers)—*M. grandoculis*; Family Mullidae (goat fish)—*M. samoensis*, *P. trifasciatus*, *P. barberinus*, *P. cyclostomus*, *U. arge*; Family Cirrhitidae (hawkfish)—*C. aprinus*; Family Chaetodontidae (butterfly fish)—*C. auriga*; Family Scorpaenidae (scorpion fish)—*S. parvipinnis*, *S. gibbosa*, *S. verrucosa*; Family Platyccephalidae (flatheads)—*Thysanophrys* sp.; Family Pomacentridae (damsel fishes)—*P. pavo*, *P. vauli*, *A. sordidus*, *A. saxatilis*, *A. lacrymatus*, *A. glaucus*, *A. leucopomus*; Family Labridae (wrasses)—*H. melapterus*, *C. gaimardi*, *C. trilobatus*, *C. chlorourus*, *P. hexataenia*, *T. lutescens*, *T. quinquevittata*, *T. umbrostigma*, *M. pardalis*, *M. meleagris*, *H. margaritaceus*, *H. trimaculatus*, *H. hoeveni*, *H. hortulanus*, *H. marginatus*, *Stethojulis* sp., *S. axillaris*; Family Gobiidae (gobies)—*B. f. fuscus*, *G. ornatus*, *G. anjerensis*; Family Eleotridae (sleepers)—*V. violifera*, *V. strigata*; Family Microdesmidae—*P. grandoculis*; Family Parapercidae (sand perch)—*P. cephalopunctatus*, *P. clathrata*; Family Blenniidae (blennies)—*A. taeniatus*, *C. sebae*, *I. paulus*; Family Brotulidae—*D. iluoceteoides*; Family Balistidae (trigger fish)—*B. viridescens*, *B. undulatus*, *P. fuscus*, *R. rectangulus*, *R. aculeatus*, *P. flavimarginatus*; Family Monacanthidae (file fish)—*A. carolae*; Family Ostracionidae (trunk fish)—*O. cubicus*; Family Tetraodontidae (puffers)—*A. hispidus*, *A. mappa*, *Arothron* sp.; Family Canthigasteridae (sharp-backed puffer)—*C. solandri*; Family Diodontidae (spiny puffer)—*D. hystric*.

Carnivores on Mid-water Fauna

Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrah*; Family Triakidae (smooth dogfishes)—*T. obesus*; Family Belonidae (needle fish)—*S. incisa*, *S. gigantea*; Family Holocentridae (squirrel fish)—*M. berndti*, *M. microphthalmus*; Family Aulostomidae (trumpet fish)—*A. chinensis*; Family Fistulariidae (cornet fish)—*F. petimba*; Family Atherinidae (silversides)—*S. temmincki*; Family Carangidae (jacks)—*T. bailloni*, *C. f. jordani*, *C. melampygus*, *E. bipinnulatus*, *S. sanctipetri*; Family Serranidae (groupers)—*V. louti*, *P. leopardus*, *P. truncatus*; Family Lutjanidae (snappers)—*Lethrinus miniatus*, *Lutjanus monostigma*, *Lut. bohar*, *Lut. vitta*, *A. virescens*; Family Blenniidae (blennies)—*A. taeniatus*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*; Family Sphyraenidae (baracudas)—*S. genie*.

Resident Roving Carnivores

Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrah*; Family Triakidae (smooth dogfish)—*T. obesus*; Family Carangidae (jacks)—*C. f. jordani*,

C. melampygus; Family Serranidae (groupers)—*P. truncatus*, *P. leopardus*.

Transient Roving Carnivores

Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrah*; Family Triakidae (smooth dogfish)—*T. obesus*; Family Carangidae (jacks)—*C. melampygus*, *E. bipinnulatus*; Family Serranidae (groupers)—*P. leopardus*; Family Lutjanidae (snappers)—*L. bohar*, *A. virescens*; Family Sphyraenidae (baracudas)—*S. genie*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*.

CORAL POLYP FEEDERS

Coelenterates, perhaps because of their nematoecysts, do not enter into the food web as intermediate forms in most marine communities, and are rarely mentioned as an influential group of organisms in the complex of ecological affairs. However, in tropical coral reefs where luxuriant coral growth not only dominates the scene as regards providing the physical habitat of countless reef species, but also comprises a substantial portion of the total animal protoplasm present (Odum & Odum, 1955), it would be strange indeed if some provision were not made within the many niches to provide for direct utilization of this food resource.

Three distinct evolutionary trends in dentition among a few families of fish have adapted them for accepting a live coral diet. For example, some butterfly fish (Chaetodontidae) and the filefish, *Oxymonacanthus*, have developed pointed, produced snouts with very small terminal mouths containing fine, incisiform, protruding teeth for biting off individual polyps above the level of the corallite. Other butterfly fish crop the polyps so closely that they scrape off the tips of the individual corallites, and parrot fish (Scaridae) have developed a strong, protruding beak of fused teeth with which they heavily scrape glomerate heads of coral, taking not only the polyps but biting deeply into the calcareous corallum as well. Other groups, particularly the trigger fish (Balistidae) and the puffers (Tetraodontidae) have developed very strong, heavy, protruding teeth (trigger fish) or have them fused into a beak as in the puffers with which the ends of ramose and cespitose coral heads (*Acropora*, *Pocillopora*, *Stylophora*) are broken off and ingested. The comparatively small amount of animal tissue in relation to the mass of skeletal material requires that such fish keep the gut well crammed with these broken tips nearly all the time.

The most important members characteristic of these three types of coral feeders are listed below:

Browsers on Coral Polyps

Family Chaetodontidae (butterfly fish)—*C. citrinellus*, *C. auriga*, *C. lunula*, *M. strigangulus*; Family Monacanthidae (file fish)—*O. longirostris*.

Grazers on Living Coral Heads

Family Chaetodontidae (butterfly fish)—*C. vagabundus*, *C. ephippium*, *C. citrinellus*; Family Scaridae (parrot fish)—*C. spinidens*, *S. sordidus*, *S. bicolor*; Unidentified scardids (7); Family Balistidae (trigger fish)—*B. undulatus*; Family Monacanthidae (file fish)—*A. carolae*.

Feeders on Branching Coral Tips

Family Balistidae (trigger fish)—*B. viridescens*, *B. undulatus*, *R. aculeatus*; Family Monacanthidae (file fish)—*A. carolae*; Family Tetraodontidae (puffers)—

A. nigropunctatus, *A. meleagris*, *A. hispidus*; Family *Canthigasteridae* (sharp-backed puffers)—*C. solandri*.

OMNIVORES

A large number of fish on Marshallese reefs have omnivorous habits, some of which are facultative omnivores and usually contain both plant and animal tissue in their digestive tracts, but do also, on occasion, take full meals of either plants or animals, whichever appears to be the most available. Another group are those fish which are primarily herbivores or primarily carnivores, but which incidentally delve into the opposite food realm, either by inadvertence through their foraging habits, or by design.

Among the facultative group, the damsel fishes (Pomacentridae), gobies (Gobiidae), trigger fish (Balistidae), and the puffers (Tetraodontidae) are the most important. Within the more incidental group the damsel fishes and parrot fishes appear to be the most important.

The lists below indicate the species examined which most clearly fall into the two categories:

Facultative Omnivores

Family Leiognathidae (silver perch)—*G. argyreus*; Family Chaetodontidae (butterfly fish)—*C. ephippium*, *C. auriga*; Family Pomacentridae (damsel fish)—*D. aruanus*, *A. sordidus*, *A. glauces*, *A. leucopomus*; Family Labridae (wrasses)—*H. hoeveni*; Family Gobiidae (gobies)—*G. anjerensis*; Family Blenniidae (blennies)—*I. paulus*, *C. sebae*; Family Balistidae (trigger fish)—*B. undulatus*, *R. rectangulus*, *R. aculeatus*; Family Monacanthidae (file fish)—*A. carolae*; Family Ostracionidae (trunk fish)—*O. cubicus*; Family Tetraodontidae (puffers)—*A. hispidus*; Family Canthigasteridae (sharp-backed puffers)—*C. solandri*.

Incidental Omnivores

Family Chaetodontidae (butterfly fishes)—*C. citrinellus*; Family Pomacentridae (damsel fishes)—*P. vauli*, *A. sazatilis*, *A. lacrymatus*, *A. dicki*, *A. biocellatus*, *A. amabilis*; Family Scaridae (parrot fishes)—*C. spinidens*, *S. sordidus*, *S. bicolor*, Unid. *Scarus* sp.; Family Tetraodontidae (puffers)—*A. mappa*.

HABITAT GROUPS ON MARSHALLESE CORAL REEFS

Anyone visiting coral reefs in the Marshall Islands will at once recognize certain characteristic associations of fishes ecologically tied to particular habitats. To analyze these natural associations we have undertaken to depict by descriptions and illustrations their essential physical and biological features.

TIDEPOOL FAUNA

For purposes of describing tidepool life on Marshallese coral reefs we have divided our account into communities living in supratidal pools, above the mean high water mark, and intertidal pools in between the mean high water mark and the mean low water mark. The supratidal pools are only found on the boulder rampart fringing the windward and semi-windward shores where the waves at high tide splash water into pools in the consolidated beach rock. The intertidal pools are found abundantly on the inner half of the seaward reef flat on the windward and semi-windward shores of the atoll.

The physical conditions in both types of tidepools are far more varied than in habitats continually sub-

merged, as tidepools are exposed not only to very high insolation from the tropical sun, but subject also to frequent periods of intense rainfall during low tides when the water in the pools becomes greatly diluted. For example, three small tidepools sufficiently within the intertidal stratum to contain small fish at Arno Atoll were checked for temperature maxima during sunny periods as the tide receded. The uppermost pool examined was awash only during the highest reaches of the incoming tide, the pool examined midway within the intertidal zone was isolated as the tide receded about half way, whereas the lowermost pool examined was awash only during strong surges at extreme low tide. On one afternoon when the air temperature was 87°F, water in the highest pool was 106°F, in the middle pool 103°F, and in the lower pool 99°F. The lower pool had received two or three tidal washes just prior to taking the temperatures. Fish in the two higher pools (*Istiblennius edentulus*, *Bathygobius f. fuscus*) were still swimming about, but in the lower pool two convict surgeon fishes (*Acanthurus t. triostegus*) and one blenny (*I. edentulus*) had died.

On a second afternoon with an air temperature of 82°F the three pools had water temperatures of 106°F, 103°F, and 106°F. No fish were dead. On a third afternoon when the air temperature was 88°F the three pools had water temperatures of 102°F, 101°F, and 101°F. The considerable variation of water temperatures in relation to air temperatures appears to result directly from the amount of cloud cover in the period just preceding the observations. The fish species inhabiting the supratidal pools are: Family Muraenidae (moray eels)—*G. pictus*; Family Acanthuridae (surgeon fishes)—*A. t. triostegus*, juveniles; Family Pomacentridae (damsel fishes)—*A. sordidus*, *A. glauces*; Family Gobiidae (gobies)—*B. f. fuscus*; Family Blenniidae (blennies)—*I. paulus*, *I. lineatus*, *I. edentulus*, *Rhabdoblennius snowi*. These species are shown in characteristic locations and activities in Fig. 2.

Fish species characteristically inhabiting an intertidal pool are: Family Pseudochromidae—*P. nigricans*; Family Acanthuridae (surgeon fish)—*A. t. triostegus*, half-grown; Family Pomacentridae (damsel fishes)—*A. sordidus*, *A. glauces*; Family Gobiidae (gobies)—*B. f. fuscus*; Family Blenniidae (blennies)—*I. paulus*, *I. lineatus*, *I. edentulus*, *Rhabdoblennius snowi*. Fish species inhabiting intertidal pools are shown in Fig. 2 in characteristic locations and activities.

In all types of tidepools on Marshallese reefs the substrate contains a heavy layer of particulate matter intermixed with short algal filaments and precipitated detritus. Because of the abundance of food of these types, herbivores and detritus feeders predominate. In each instance, however, a few carnivores occur; the tideflat moray, *G. pictus*, and the voracious pseudochromid, *P. nigricans*, being the most important. Supratidal pools frequently serve as comparatively safe rearing ponds for species such as the convict surgeon fish, *A. t. triostegus*. However, a considerable mortality occurs in this species when water temperatures range over 100°F.

SEAWARD REEF FLAT FAUNA

The outer half of the seaward reef flat slopes just perceptibly downward to the back ridge trough which is a slightly depressed area always covered with water. Immediately seaward of the back ridge trough is the elevated coralline ridge. A vertical section showing the elevations of the seaward reef flat at Arno Atoll in

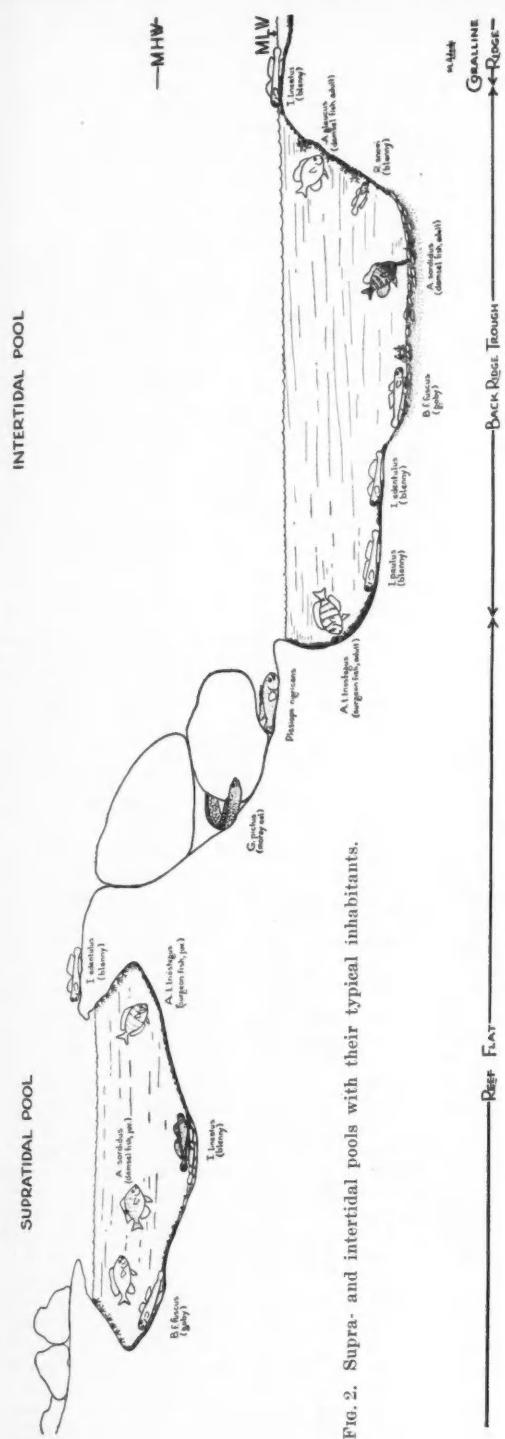


FIG. 2. Supra- and intertidal pools with their typical inhabitants.

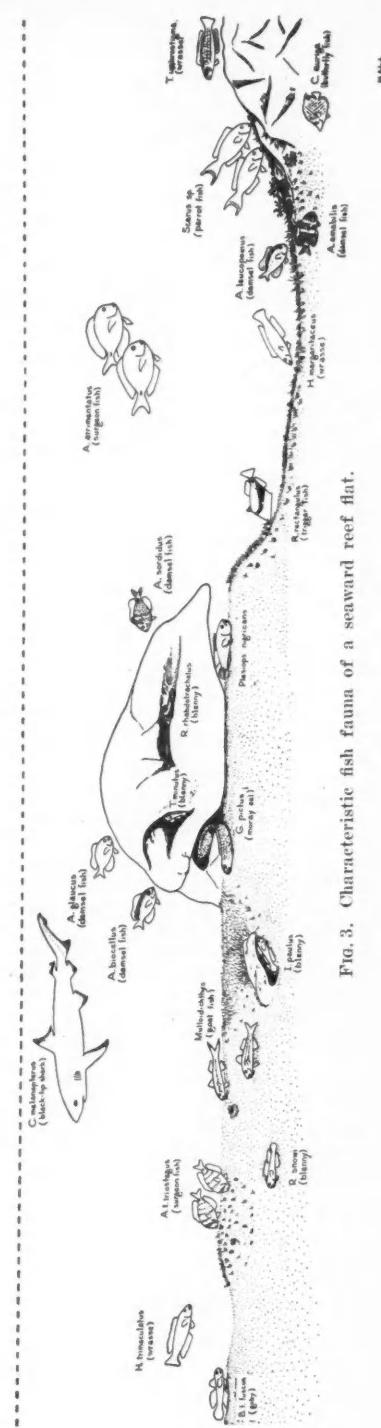


FIG. 3. Characteristic fish fauna of a seaward reef flat.

relation to mean sea level has been worked out and submitted for publication (Hiatt, in press).

The outer half of the seaward reef flat is always covered at mean sea level, and is exposed only on certain spring lows, and then only for a few minutes. Ordinarily, the sea swell is adequate to send waves of translation over it even when the tide is exceedingly low. The variations in salinity and temperature are far less than those characteristic for the inshore half of the reef flat.

During low water very little activity, except for the smaller organisms, is evident in this area of the reef. However, as soon as the tide rises sufficiently this region is actually inundated by a horde of larger fish, among them large schools of parrot fish, surgeon fish, goat fish, and small, widely ranging sharks. This intense activity ensues until the water recedes, and these roving types then move out and over the coralline ridge to await along the reef front for the next tidal rise.

The characteristic fishes of this habitat are shown in Fig. 3, and listed below: Family Carcharhinidae (gray sharks)—*C. melanopterus*; Family Muraenidae (moray eels)—*G. pictus*; Family Pseudochromidae—*P. nigricans*; Family Mullidae (goat fishes)—*M. samoensis*, *U. arge*; Family Chaetodontidae (butterfly fishes)—*C. auriga*; Family Acanthuridae (surgeon fishes)—*A. nigrofasciatus*, *A. t. triostegus*; Family Pomacentridae (damsel fishes)—*A. sordidus*, *A. glaucus*, *A. biocellatus*, *A. amabilis*, *A. leucopomus*; Family Labridae (wrasses)—*T. umbrostygma*, *H. marginatus*, *H. trimaculatus*; Family Scaridae (parrot fish)—Several unidentified species of *Scarus*; Family Gobiidae (gobies)—*B. f. fuscus*; Family Blenniidae (blennies)—*I. paulus*, *Rhabdoblennius rhabdotrachelus*; Family Tripterygiidae—*Tripterygion minutus*.

FAUNA OF THE SURF ZONE AND SURGE CHANNELS

The fish fauna of the outer reef edge and the surge channels, especially on leeward ocean reefs is so varied and complex that it defies adequate description and characterization. A view into one of these surge channels and out over the steep seaward slope is truly one of the most spectacular to be experienced by man. The reef edge and slope are almost solidly covered by over one hundred species of corals of all shapes and hues, and the density and diversity of the fish fauna is exceedingly great. We have made a very feeble attempt at depicting such a scene in Fig. 4.

Because it is manifestly impractical to try to list the fish fauna of this zone, we have selected for presentation only those types most influential in this community. Their characteristic positions and activity are shown in the accompanying figure. Two species are so characteristic of the breaker zone, the sweeper, *Pempheris ovalensis*, and the surgeon fish, *Acanthurus guttatus*, that they are here given special notation. *A. guttatus* particularly can be seen in large, fast-swimming schools in the white water of the breaking waves. The sweepers usually occupy positions near the head of shallow channels or just below the white water. The most important species in this habitat are listed below: Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrah*; Family Triakidae (smooth dogfishes)—*T. obesus*; Family Muraenidae (moray eels)—*G. javanicus*; Family Cirrhitidae (hawkfish)—*A. arcatus*, *P. forsteri*; Family Serranidae (groupers)—*E. merra*, *P. leopardus*, *P. truncatus*; Family Pseudochromidae—*P. tapeinosoma*; Family Lutjanidae (snappers)—*L. gibbus*; Family Sparidae

(snappers)—*M. grandoculis*; Family Acanthuridae (surgeon fishes)—*A. achilles*, *A. aliale*, *A. nigrofasciatus*, *A. lineatus*, *N. lituratus*, *N. unicornis*, *Z. veliferum*; Family Pomacentridae (damsel fishes)—*A. lacrymatus*; Family Labridae (wrasses)—*H. marginatus*; Family Scaridae (parrot fishes)—*Scarus* sp. (several); Family Blenniidae (blennies)—*C. sebae*, *C. variolosus*; Family Balistidae (trigger fish)—*R. rectangulus*.

FISH FAUNA ASSOCIATED WITH ALGAE

Earlier in this report the algal feeders were considered from the standpoint of their actual foraging methods. In this section we shall consider the herbivores as regards their associations with different types of algae growing on both rocky and compacted sandy substrates. The important herbivores in this reef association are shown in their characteristic localities and activities in Fig. 5.

Among the algal feeders are a few which scoop up the surface benthos, sift it to remove the unicellular algae with some admixed detritus for ingestion, and reject the remainder either through the mouth or gill opening. The mullets, *N. chaptali* and *C. crenilabis*, feed entirely in this manner, and can be seen in schools sucking up and sifting the fine benthos on the sandy bottoms.

A rather large group of surgeon fish feeds exclusively on the short filaments of algae growing on the compacted sand. To do this schools of them literally stand on their heads and busily graze on the bottom. Species such as *A. mata*, *A. xanthopterus*, *A. gahhm*, and *A. olivaceus* forage in this manner.

Most herbivores browse or graze algae growing on rocky surfaces. Some browse only the larger seaweeds, while many browse and graze the shorter filaments. Among the most important browsers which bite off fronds and filaments from algae growing on rocky surfaces are: rabbit fish (Siganidae), pilot fish (Kyphosidae), butterfly fish (Chaetodontidae), surgeon fish (Acanthuridae), damsel fish (Pomacentridae), and trigger fish (Balistidae). The kinds of algae taken are shown diagrammatically in Fig. 5 and the species are listed in detail under the section on algal feeders considered earlier in this paper.

FISH FAUNA ASSOCIATED WITH LEDGES AND CAVERNS

A swimmer approaching a coral bed is immediately aware of, and greatly impressed by, the large number and variety of fish he sees. However, only a small part of the fish fauna is then in evidence, because most are concealed under rocks or ledges, or are hiding in holes and caverns in the coral itself. It is only after intense searching that some of these species become evident, and only after the area has been poisoned with rotenone that the full impact of the concealed species is felt. No special figure was prepared to show only these species as many of them are visible in our illustrations of other reef situations.

A very large group which remains concealed in coral patches and in rubble is the moray eels. These are primarily ledge and hole dwellers. Another important segment of the fish fauna which inhabits caverns is the squirrel fishes (Holocentridae) which never venture far from their caverns, and usually are seen only in them. They are curious about swimmers, however, and if one watches the opening of a cavern he will see them come up, usually one at a time, take a good look at the swimmer and then disappear again. Also living



FIG. 4. The fish fauna of a surge channel and the surf zone.

in holes in the coral and in small caverns are many species of cardinal fish (Apogonidae) which frequently hover inside caverns in exceedingly large schools, only venturing out if there is no danger foreseen.

Under ledges and pedestal coral colonies live solitary demersal groupers (Serranidae) of many species, but with similar lying-in-wait foraging techniques, having only the head extended from beneath cover. Although several species of snappers (Lutjanidae) characteristically hide under large coral heads or in ledges, they are not demersal and do not lie in wait for prey. Instead, they forage just a short distance away from their refuge.

A number of the butterfly fishes (Chaetodontidae) also frequent caverns or stay below large coral heads a good deal of the time. Two species holding great attraction for, as well as commanding great respect from, reef biologists are the turkey or lion fish, *Pterois volitans* and *P. radiata*. These venomous species, having greatly elaborated fins and striking coloration, seclude themselves under ledges or corals and have never been seen by us in an exposed situation.

Observations made on the reefs, coupled with a check on the proportion of empty stomachs in fishes caught during the day, indicate that certain of these ledge and cavern dwellers probably have nocturnal foraging propensities. These species are: Family Muraenidae (moray eels)—*G. pictus*, *G. flavimarginatus*, *G. undulatus*, *G. fimbriatus*; Family Holocentridae (squirrel fishes)—*M. berndti*, *M. microphthalmus*, *H. sammarus*, *H. lacteoguttatus*, *H. microstomus*, *H. laevis*, *H. diadema*, *H. spinifer*.

Ledge and cavern dwellers known to be day foragers are: Family Muraenidae (moray eels)—*E. zebra*, *E. leucotaenia*, *E. polyzona*, *U. xanthopterus*, *R. marshallensis*, *G. javanicus*, *G. buroensis*, *G. margaritophorus*; Family Congridae (conger eels)—*C. noordziedi*; Family Apogonidae (cardinal fishes)—*A. novemfasciatus*, *A. snyderi*, *A. exostigma*, *A. nigrofasciatus*, *A. novaegeorgiae*, *A. erythrinus*, *P. quinque-lineata*; Family Priacanthidae (big eyes)—*P. cruentatus*; Family Serranidae (groupers)—*E. merra*, *E. fusco-guttatus*, *E. kohleri*, *E. hexagonatus*, *E. macrospilos*, *E. spilotus*, *V. louti*, *C. argus*, *C. urodon*, *A. leucogrammicus*, *P. truncatus*; Family Pempheridae (sweepers)—*P. ovalensis*; Family Lutjanidae (snappers)—*L. monostigma*, *L. vitta*, *L. vaigiensis*, *L. gibbus*; Family Chaetodontidae (butterfly fish)—*C. vagabundus*, *C. ephippium*, *C. auriga*, *C. lunula*, *C. flavissimus*, *M. strigangulus*; Family Acanthuridae (surgeon fishes)—*C. striatus*, *A. mata*; Family Scorpaenidae (scorpion fishes)—*P. radiata*, *P. volitans*; Family Brotulidae—*D. iluococtoides*.

FISH FAUNA ASSOCIATED WITH MID-WATER AND SURFACE COMMUNITIES

Surface and mid-water communities are comparatively distinct, although some larger carnivores range rather widely and enter both areas on occasion. Surface communities are composed primarily of minute zooplankton, larger zooplankton, small plankton-feeding fish, (the round herring, *S. delicatulus*, and silversides, *A. ovalaua* and *P. pinguis*), larger macroplankton feeding fish such as the half-beaks (Hemiramphidae), trumpet fish (Aulostomidae), cornet fish (Fistulariidae), and fish-eating carnivores such as needle fish (Belontidae), tunas (Scombridae), barracuda (Sphyraenidae), and rainbow runner (Carangidae).

In mid-water a number of large, hovering groupers (Serranidae) and snappers (Lutjanidae) occur just above the bottom, and several species of more rapidly swimming roving carnivores such as sharks (Carcharhinidae and Triakidae), jacks (Carangidae), and snappers (Lutjanidae) are usually always present in quiet waters on all reefs. Fig. 6 depicts the important species engaging in their usual activities in the characteristic habitat.

The important species in the surface community are listed below: Family Mobulidae (manta rays)—*M. alfredi*; Family Dussumieriidae (round herrings)—*S. delicatulus*; Family Belontidae (needle fishes)—*S. incisa*, *S. gigantea*; Family Hemiramphidae (half-beaks)—*H. affinis*, *H. laticeps*; Family Atherinidae (silversides)—*A. ovalaua*, *P. pinguis*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*; Family Sphyraenidae (barracuda)—*S. genie*; Family Carangidae—*S. sanctipetri*.

The important species in the mid-water community are the following: Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrah*; Family Triakidae (smooth dogfishes)—*T. obesus*; Family Holocentridae (squirrel fishes)—*M. berndti*, *M. microphthalmus*; Family Aulostomidae (trumpet fish)—*A. chinensis*; Family Fistulariidae—*F. petimba*; Family Atherinidae (silversides)—*S. temmincki*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*; Family Sphyraenidae (barracuda)—*S. genie*; Family Carangidae (jacks)—*T. bailloni*, *C. f. jordani*, *C. melampygus*, *S. sanctipetri*, *B. bipinnulatus*; Family Serranidae (groupers)—*V. louti*, *P. leopardus*, *P. truncatus*; Family Lutjanidae (snappers)—*L. monostigma*, *L. bohar*, *L. vitta*, *A. virescens*, *L. miniatus*.

FISH FAUNA ASSOCIATED WITH GLOMERATE CORAL HEADS

Because glomerate coral heads are generally devoid of interstices in which small organisms can hide, such heads are visited only by fish species intent upon browsing or grazing coral polyps. Most glomerate heads (*Porites*, *Astroopora*, *Coscinaraea*, *Cyphastrea*, *Goniastrea*, *Leptastrea*, *Pavona*) on luxuriant coral reefs are marred by paired tooth scrapings as a result of grazing on them by parrot fishes, trigger fishes, and others. Frequently such tooth marks are exceedingly abundant, indicating that the turnover rate of corals and coral feeding fishes must be running rather close to maximum sustaining capacity.

Fishes which browse the polyps without cropping too closely and getting particles of the calcareous corallite and corallum belong mostly to the family Chaetodontidae (butterfly fish). The most important grazers are the parrot fishes (Scaridae), the trigger fishes (Balistidae), and the puffers (Tetraodontidae).

Fig. 7 depicts the fish activity around a glomerate coral head. The significant species associated with such coral heads, all grazers or browsers except the pipe fish which merely hunt for small crustaceans on the surface of the head, are listed below: Family Syngnathidae (pipe fishes)—*C. i. waitei*, *C. f. conspicillatus*; Family Chaetodontidae (butterfly fishes)—*C. vagabundus*, *C. ephippium*, *C. citrinellus*, *C. auriga*, *C. lunula*, *M. strigangulus*; Family Scaridae—*C. spinidens*, *S. sordidus*, *S. bicolor*, *Scarus* sp. (? unid. species); Family Balistidae (trigger fish)—*B. undulatus*; Family Tetraodontidae (puffers)—*A. meleagris*.

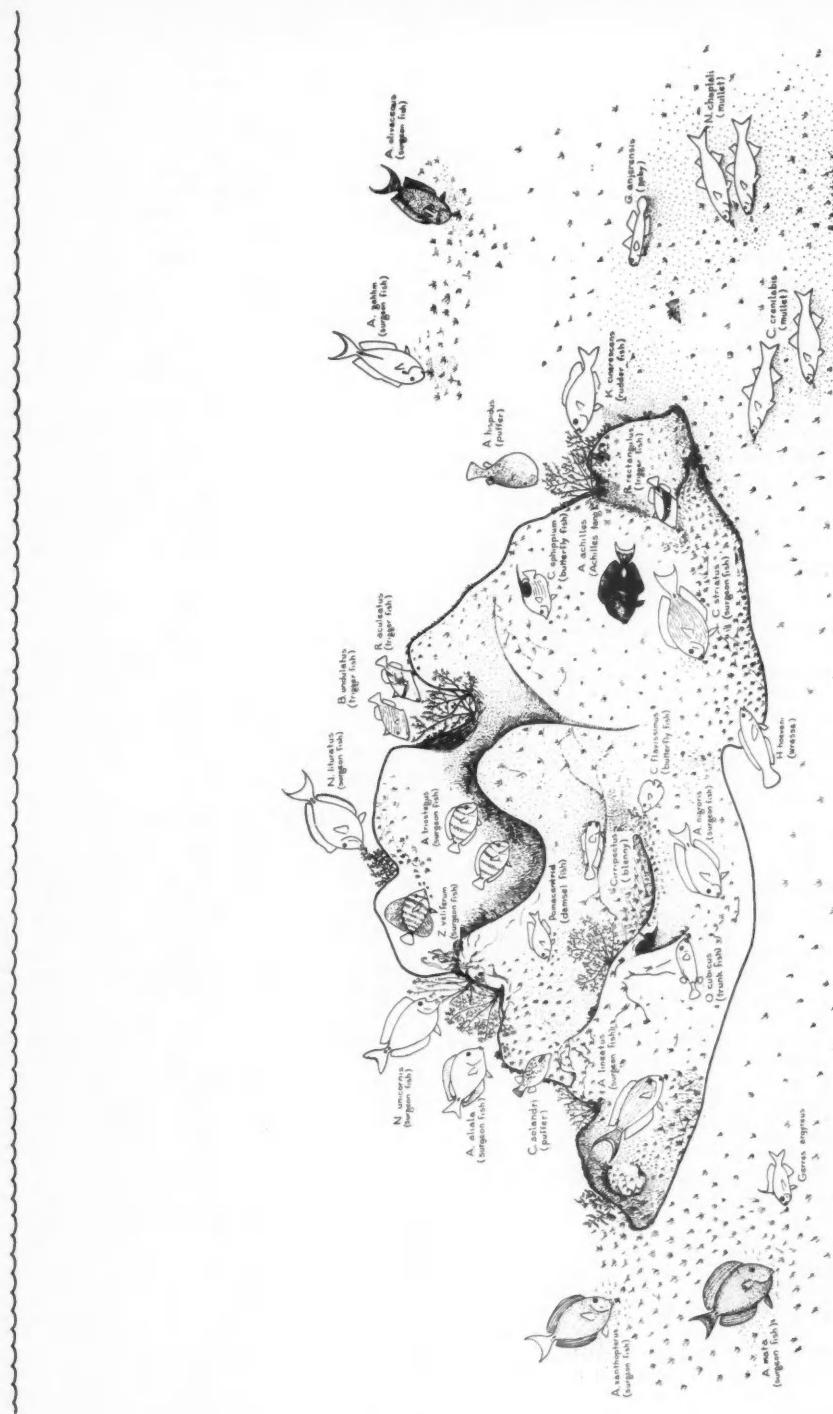


FIG. 5. Herbivorous fish in characteristic feeding attitudes.

FISH FAUNA ASSOCIATED WITH RAMOSE CORALS
AND THEIR DEAD BASES

An abundant fauna and flora are associated with branching or ramoso types of coral heads. Not only is the coral head itself (polyps and contained zooxanthellae together with the filamentous algae living in the skeleton) almost a wholly contained ecological unit as stated by Odum & Odum (1955), but if we include the animal populations intimately associated with a branching head, it is even more complete as a contained ecological unit, and would justify community status by itself. Aside from the coral tissues themselves, there are among the fish associated with a single ramoso head herbivores, carnivores, and omnivores. When we include the plethora of invertebrate types the community becomes more complex and complete. No doubt, a careful study of the microflora would reveal that it contains an adequate population of reducers too!

We have depicted the more important life about two types of ramoso corals in Fig. 8. Comparatively few organisms are found in the interstices of the pedestal colonies of ramoso corals because of their more exposed aspect. However, a number of species take refuge beneath the explanate head, and a large number of coral polyp feeders find such heads attractive because the branchlets are easily broken off, and, for some species, the terminal polyps are especially vulnerable for cropping.

In the ramoso and cespitose heads with long branches, the interstices are attractive places of refuge for small crabs, shrimps, polychaetes, clams, and fishes. A number of highly carnivorous fish live within the interstices (*Gobiodon* spp., *Paragobiodon* spp., *Caranxanthus* spp.) and do not venture outside the head. Other fishes such as the damsel fishes, *Dascyllus aruanus*, *Chromis caeruleus*, and *C. atripeptoralis*, use the interstices only for protection, and swarm about just outside the head feeding on the abundant plankters. A number of carnivores such as the wrasses, *Gomphosus varius*, and *Epibulus insidiator*, and the butterfly fish, *Forcipiger longirostris*, have snouts either highly protractile or very elongate for probing deeply into the interstices in search of prey. Other wrasses constantly poke about amongst the branches searching for small crustaceans within reach.

On the bases of most of these heads algal filaments grow as a thin veneer. A number of herbivorous and omnivorous species graze and browse this material.

The following species are important members of the community of organisms associated with ramoso coral heads:

Herbivores

Family Chaetodontidae (butterfly fishes)—*C. reticulatus*, *C. flavissimus*; Family Pomacentridae (damsel fishes)—*A. dicki*.

Carnivores

Family Muraenidae (moray eels)—*U. xanthopterus*, *R. marshallensis*, *G. buroensis*, *G. margaritophorus*, *G. fimbriatus*; Family Holocentridae (squirrel fishes)—*H. sammara*, *H. microstomus*, *H. laevis*, *H. diadema*, *H. spinifer*; Family Syngnathidae (pipefishes)—*C. i. waiteti*, *C. f. conspicillatus*; Family Apogonidae (cardinal fishes)—*A. novemfasciatus*, *A. snyderi*, *A. exostigma*, *A. nigrofasciatus*, *A. novaeguineae*, *A. erythrinus*, *G. philippinus*, *P. quinquecincta*; Family Serranidae (groupers)—*C. urodelus*; Family Pseudochromidae—*P.*

melas, *P. polycantha*, *P. tapeinosoma*; Family Pempheridae (sweepers)—*P. oualensis*; Family Lutjanidae (snappers)—*S. cancellatus*; Family Cirrhitidae (hawkfish)—*A. arcatus*, *P. forsteri*, *C. aprinus*, *C. pinnulatus*; Family Scorpaenidae (scorpion fishes)—*S. parvipinnis*; Family Caracanthidae—*C. unipinnus*; Family Pomacentridae (damsel fishes)—*C. caeruleus*, *C. atripeptoralis*; Family Labridae (wrasses)—*G. varius*, *C. oxycephalus*, *T. hardwickei*, *T. quinquevittata*, *E. insidiator*, *H. marginatus*, *N. taeniourus*; Family Gobiidae (gobies)—*G. rivulatus*, *G. erythrosipilus*, *P. echinocephalus*; Family Balistidae (trigger fish)—*B. viridescens*; Family Monacanthidae (file fishes)—*O. longirostris*; Family Tetraodontidae (puffers)—*A. nigropunctatus*, *A. meleagris*.

Omnivores

Family Chaetodontidae (butterfly fishes)—*C. citrinellus*, *C. auriga*; Family Pomacentridae (damsel fish)—*D. aruanus*; Family Labridae (wrasses)—*T. lutescens*, *S. axillaris*; Family Balistidae (trigger fish)—*R. aculeatus*, *B. undulatus*; Family Monacanthidae (file fish)—*A. carolae*; Family Tetraodontidae (puffers)—*A. hispidus*; Family Canthigasteridae (sharp-backed puffers)—*C. solandri*.

TROPHIC LEVELS

One of the prime objectives of this study was to determine to which trophic levels the more important fish species belonged. Moreover, among reef ecologists there has always been some question as to reasons why such an apparently large fish population could exist when the primary producers in evidence seemed to be far less abundant than they should be on theoretical grounds, as interpreted from a pyramid of biomass based on the standing crop. This latter question has been solved to a great extent at least by the brilliant research of Odum & Odum (1955) on Eniwetok reefs. There they found that in the living coral heads themselves the zooxanthellae contained in the tissues of polyps and, even more important, the filamentous algae growing in the pores of the inert skeleton in bands below the outer living animal tissue, actually made the coral head more plant than animal, i.e., more producer than consumer, by a ratio of about 3 to 1. In addition to the algae contained in coral heads, there is considerable filamentous algae in the sand, shingle or rubble, dead coral heads, and the porous reef floor, as well, of course, as in the algal mats and seaweed visible to the naked eye. As Odum & Odum (1955) point out, "From the standpoint of the entire reef ecosystem it does not matter how much food made by algae within the live coral head [or within porous rock, rubble, and sand] is used by coral animals [or other animals] directly. Only by considering the large amount of producer tissue in [these subsurface locations] it is possible to explain the great preponderance of organisms classed as animals."

The second important consideration in the balance sheet of the coral reef ecosystem is the fact that most of the fish protoplasm visible to a swimmer represents herbivorous types belonging to the second trophic level. Moreover, on a more quantitative basis, although admittedly rough, Odum & Odum (1955) found that among the fishes there was a striking predominance on a weight

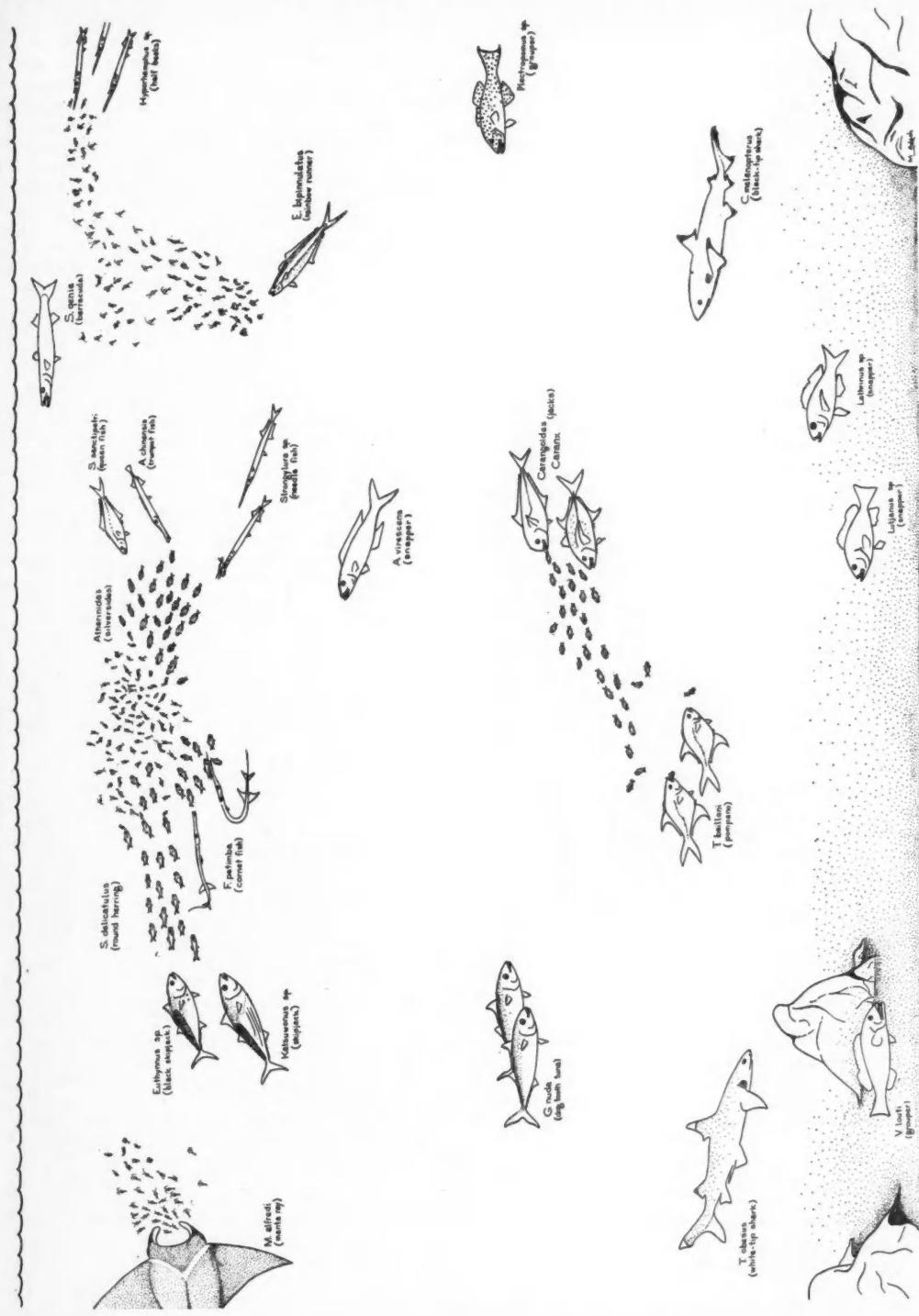


FIG. 6. The mid-water and surface community.

basis of herbivorous parrot fishes, surgeon fishes, damsel fishes, and butterfly fishes in comparison to the wrasses, groupers, and other carnivores. The energetics of the system at this level are the most favorable in the entire food chain, regardless of the actual quantitative efficiency, since the herbivores are dependent upon the primary producers which, as in other ecosystems, have a much greater biomass than the carnivorous levels toward the apex of the pyramid.

Phylogenetically, certain interesting situations appear which are noteworthy. Our studies indicate that the more advanced and specialized fishes appear to be heading morphologically and physiologically toward the lower trophic levels where the stored energy in terms of food supply is in greater quantity. Note, for example, the foraging habits of the trigger fish (Balistidae), puffers (Tetraodontidae), etc., which have become omnivorous and frequently make entire meals on algae as well as on many little used invertebrates such as the sponges, coelenterates, echinoderms, and tunicates. Conversely, the most primitive fishes in the phylogenetic scale are exclusively carnivores, and usually so at the fourth or fifth trophic levels where comparatively little food is available. The more generalized species appear to fall mostly in the third and fourth trophic levels where a considerable amount of comparatively easy to get food items is available to them in the form of invertebrates or small fishes of the second and third trophic levels. The invertebrates comprise the greatest biomass of the second trophic level (Odum & Odum, 1955), and, although their detailed food habits are not accurately known, we are able to assign them arbitrarily to the second trophic level for the most part, although some comprise a portion of the third trophic level.

The fish families which comprise the bulk of the biomass at the second trophic level, surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), and rabbit fishes (Siganidae) are rather highly evolved, specialized fishes also. The dental and other morphological modifications and physiological changes from the more primitive type fish are considerable, and these did not evolve in spite of the great mass of plant food available until comparatively lately as regards the evolutionary time scale of the group. It is still an enigma why the biomass of herbivorous fishes is so proportionately great on tropical reefs where larger seaweeds are not abundantly available, and so proportionately small along coastal shores in the temperate and arctic seas.

At the present time research on the primary producers of coral reef ecosystems in the Marshall Islands has reached a comparatively high level of understanding. The present studies should provide the framework for far greater knowledge at the higher trophic levels for the higher organisms, but there still remains to be known the role of the myriads of invertebrates which inhabit the reefs.

Below are listed the species comprising the several trophic levels on Marshallese reefs. It should be borne in mind that the trophic level into which a particular carnivore is placed frequently depends upon its growth stage. Many juvenile carnivores occupy a trophic level one or two levels below that eventually occupied as an adult. These changes have been taken into consideration when borne out by our analysis of their food and feeding habits.

First Trophic Level (Primary Producers) Algae

Second Trophic Level (Primary Consumers; Herbivores)

Family Mugilidae (mullets)—*Crenimugil crenilabis*, *Neomyxus chapitali*; Family Leiognathidae (silver perch)—*Gerres argyreus*; Family Siganidae (rabbit fishes)—*Siganus rostratus*; Family Kypnosidae (pilot fish)—*Kyphosus cinerascens*; Family Chaetodontidae (butterfly fishes)—*Chaetodon auriga*, *C. ephippium*, *C. reticulatus*, *Centropyge flavissimus*; Family Acanthuridae (surgeon fishes)—*Acanthurus achilles*, *A. alia*, *A. nigroris*, *A. xanthopterus*, *A. guttatus*, *A. lineatus*, *A. mata*, *A. gahm*, *A. olivaceus*, *A. t. triostegus*, *Ctenochaetus striatus*, *Naso lituratus*, *N. unicornis*, *Zebrazoma veliferum*; Family Pomacentridae (damsel fishes)—*Abudefduf amabilis*, *A. biocellatus*, *A. dicki*, *A. glauces*, *A. lacrymatus*, *A. leucopomus*, *A. saxatilis*, *A. septemfasciatus*, *A. sordidus*, *Dascyllus aruanus*, *Pomacentrus albofasciatus*, *P. jenkinsi*, *P. nigricans*, *P. vauli*; Family Labridae (wrasses)—*Halichoeres hoeveni*; Family Blenniidae (blennies)—*Cirripectes sebae*, *C. variolosus*, *Ezallias brevis*, *Istiblennius coronatus*, *I. paulus*; Family Balistidae (trigger fishes)—*Balistapus undulatus*, *Melichthys vidua*, *Rhinecanthus aculeatus*, *R. rectangularis*; Family Monacanthidae (file fishes)—*Amanses carolae*; Family Ostracionidae (trunk fishes)—*Ostracion cubicus*; Family Tetraodontidae (puffers)—*Arothron hispidus*; Family Canthigasteridae (sharp-backed puffers)—*Canthigaster solandri*.

Third Trophic Level (Secondary Consumers; Carnivores)

Family Mobulidae (manta rays)—*Manta alfredi*; Family Dussumieriidae (round herrings)—*Spratelloides delicatulus*; Family Clupeidae (sardines)—*Harengula kunzei*; Family Ophichthidae (snake eels)—*Brachysomophis sauropsis*; Family Muraenidae (moray eels)—*Echidna leucotaenia*, *E. polyzona*, *E. zebra*, *Gymnothorax bueroensis*, *G. flavimarginatus*, *G. javanicus*, *G. marginatus*, *G. pectoralis*, *Rabula marshallensis*, *Uropterygius xanthopterus*; Family Congridae (conger eels)—*Conger noordzicki*; Family Moringuidae (whip eels)—*Moringua macrochir*; Family Synodontidae (lizard fish)—*Synodus variegatus*; Family Hemiramphidae (half-beaks)—*Hyporamphus affinis*, *H. laticeps*; Family Bothidae (flounders)—*Bothus mancus*; Family Holocentridae (squirrel fishes)—*Holocentrus diadema*, *H. lacteoguttatus*, *Holocentrus lacvis*, *H. microstomus*, *H. spinifer*, *Myripristes berndti*, *M. micropthalmus*; Family Syngnathidae (pipefishes)—*Corythoichthys flavofasciatus conspicillatus*, *C. intestinalis waitei*; Family Atherinidae (silversides)—*Pranesus pinguis*, *Allanetta ovalana*, *Stenatherina temmincki*; Family Polynemidae (threadfins)—*Polydactylus sexfiliis*; Family Carangidae (jacks)—*Elagatis bipinnulatus*, *Trachurops crumenophthalmus*; Family Apogonidae (cardinal fishes)—*Apogon erythrurus*, *A. exostigma*, *A. nigrofasciatus*, *A. novaequinea*, *A. snyderi*, *Cheilodipterus macrodon*, *Gymnapogon philippinus*; Family Serranidae (groupers)—*Cephalopholis argus*, *C. urodelus*, *Epinephelus hexagonatus*, *E. maculipinnis*, *E. merra*, *E. spiloto*, *Variola louti*; Family Pseudochromidae—*Plesiops melas*, *P. nigricans*, *Pseudochromis tapeinosoma*, *Pseudogramma polyacanthus*; Family Pempheridae (sweepers)—*Pempheris oualensis*; Family Lutjanidae (snappers)—*Gnathodentex aureolineatus*, *Gymnocranius griseus*, *Lutjanus gibbus*, *L. vaigiensis*, *L. vitta*, *Scolopsis cancellatus*; Family Leiognathidae (silver perch)—*Gerres argyreus*; Family

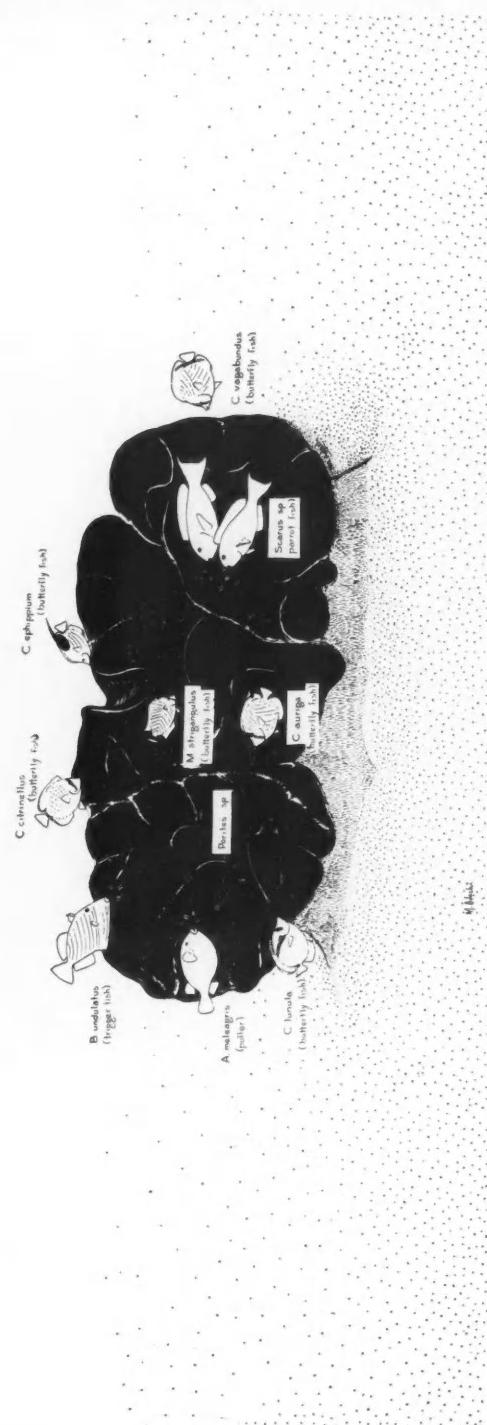


FIG. 7. Feeders upon glomerate corals.

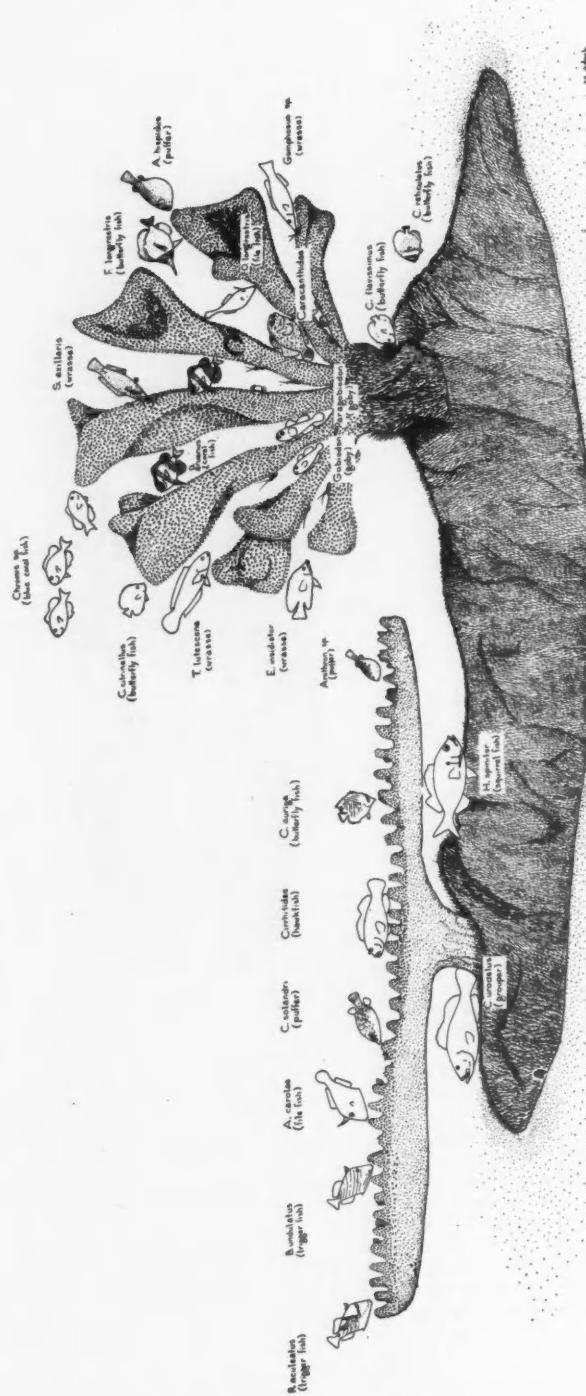


FIG. 8. Fishes associated with ramose corals.

Sparidae (snappers)—*Monotaxis grandoculis*; Family Mullidae (goat fishes)—*Mulloidichthys samoensis*, *Parupeneus barberinus*, *P. trifasciatus*, *Upeneus argus*; Family Cirrhitidae (hawkfish)—*Amblycirrhitus arcatus*, *Cirrhichthys aprinus*, *Cirrhitus pinnulatus*; Family Chaetodontidae (butterfly fishes)—*Chaetodon auriga*; Family Scorpaenidae (scorpion fish)—*Pterois radiata*, *P. volitans*, *Scorpaenodes parvipinnis*; Family Caracanthidae—*Caracanthus unipinnus*; Family Platyccephalidae (flatheads)—*Thysanophrys* sp.; Family Pomacentridae (damsel fish)—*Abudefduf glaucus*, *A. lacrymatus*, *A. leucopomus*, *A. saxatilis*, *A. septemfasciatus*, *A. sordidus*, *Dascyllus aruanus*, *Chromis atripinnoralis*, *C. caeruleus*, *Pomacentrus pavo*; Family Labridae (wrasses)—*Cheilinus chlorourus*, *C. oxycephalus*, *C. trilobatus*, *Coris angulata*, *C. gaimardi*, *Epibulus insidiator*, *Gomphosus varius*, *Halichoeres hoeschei*, *H. hortulanus*, *H. marginatus*, *H. trimaculatus*, *Hemigymnus melapterus*, *Labrodes dimidiatus*, *Macropharyngodon meleagris*, *M. pardalis*, *Novaculichthys taeniourus*, *Pseudochelichthys hexataenia*, *Stethojulis axillaris*, *Stethojulis* sp., *Thalassoma hardwickei*, *T. lucasanum marnae*, *T. lutescens*, *T. quinquevittata*, *T. umbrostigma*; Family Gobiidae (gobies)—*Bathygobius f. fuscus*, *Gnatholepis anjerensis*, *Gobiodon rivulatus*, *G. erythrosipilus*, *Gobius ornatus*, *Paragobiodon echinocephalus*; Family Eleotridae (sleepers)—*Valenciennea strigata*, *V. violacea*; Family Microdesmidae—*Paragobiooides grandoculis*; Family Parapercidae (sand perch)—*Parapercis cephalopunctatus*, *P. clathrata*; Family Blenniidae (blennies)—*Cirripectes sebae*, *Istiblennius paulus*; Family Brotulidae—*Dinemantichthys iluocoteoides*; Family Balistidae (trigger fish)—*Balistapus undulatus*, *Pseudobalistes flavimarginatus*, *P. fuscus*, *Rhinecanthus aculeatus*, *R. rec-*

tangulus; Family Ostracionidae (trunk fishes)—*Ostracion cubicus*; Family Tetraodontidae (puffers)—*Arothron hispidus*, *A. mappa*; Family Diodontidae (spiny puffers)—*Diodon hystrix*.

Fourth Trophic Level (Tertiary Consumers; Carnivores)

Family Carcharhinidae (gray sharks)—*Carcharhinus melanopterus*, *C. menisorrah*; Family Triakidae (smooth dogfishes)—*Triakodon obesus*; Family Muraenidae (moray eels)—*Gymnothorax javanicus*, *G. flavimarginatus*, *G. undulatus*; Family Synodontidae (lizard fishes)—*Synodus variegatus*, *Saurida gracilis*; Family Belontidae (needle fishes)—*Strongylura incisa*, *S. gigantea*; Family Hemiramphidae (half-beaks)—*Hyporamphus laticeps*; Family Bothidae (flounders)—*Bothus mancus*; Family Holocentridae (squirrel fishes)—*Holocentrus microstomus*; Family Aulostomidae (trumpet fishes)—*Aulostomus chinensis*; Family Fistulariidae (cornet fishes)—*Fistularia petimba*; Family Carangidae (jacks)—*Trachinotus bailloni*, *Caranoides ferdau jordani*, *Caranx melampygus*; Family Apogonidae (cardinal fishes)—*Apogon novemfasciatus*, *Paramia quinquelineata*; Family Priacanthidae (big eyes)—*Priacanthus cruentatus*; Family Serranidae (groupers)—*Epinephelus merra*, *E. fuscochattatus*, *E. kohleri*, *E. hexagonatus*, *E. macrospilus*, *E. spilotus*, *Variola louti*, *Cephalopholis argus*, *Anperodon leucogrammicus*, *Plectropomus truncatus*; Family Pseudochromidae—*Plesiops melas*; Family Pempheridae (sweepers)—*Pempheris ovalensis*; Family Lutjanidae (snappers)—*Lutjanus monostigma*, *L. bohar*, *L. vitta*, *L. gibbus*, *Lethrinus microdon*; Family Mullidae (goat fishes)—*Parupeneus cyclostomus*; Family Cirrhitidae (hawkfishes)—*Paracirrhites forsteri*; Family Chaetodontidae (butterfly fishes)—*Chaetodon vag-*

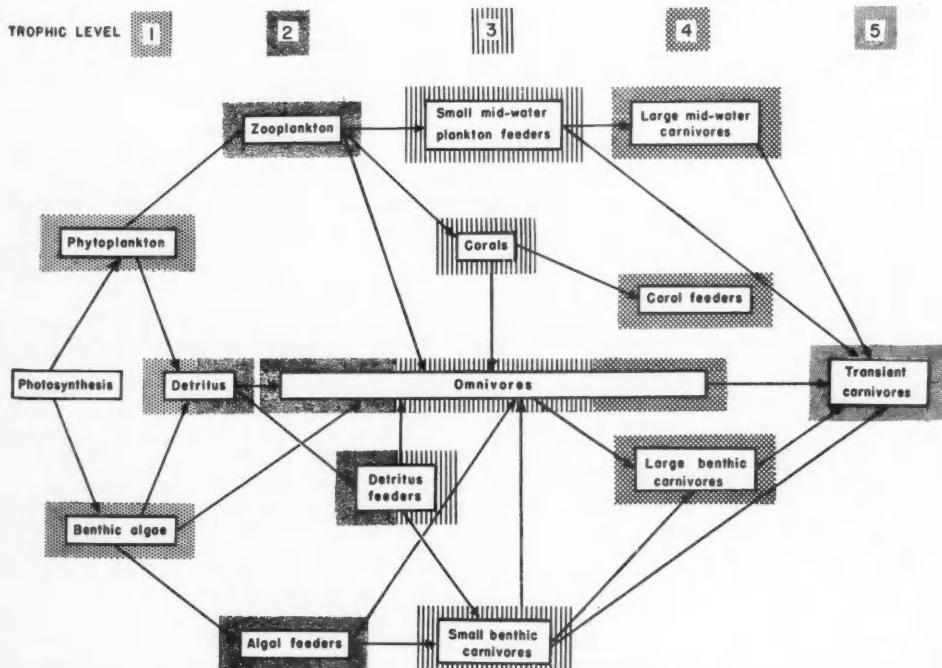


FIG. 9. The food web of Marshallese reefs.

bundus, *C. ephippium*, *C. citrinellus*, *C. auriga*, *C. lunula*, *Megaprotodon strigangulus*; Family Scorpaeidae (scorpion fishes)—*Scorpaenopsis gibbosa*, *Synanceja verrucosa*; Family Serridae (parrot fishes)—*Cryptotomus spinidens*, *Scarus sordidus*, *S. bicolor*; Family Parapercidae (sand perches)—*Parapercis cephalopunctatus*, *P. clathrata*; Family Blenniidae (blennies)—*Aspidontus taeniatus*; Family Balistidae (trigger fishes)—*Balistoides virides*, *Balistapus undulatus*; Family Monacanthidae (file fishes)—*Amanse carolae*, *Oxymonacanthus longirostris*; Family Tetraodontidae (puffers)—*Arothron nigropunctatus*, *A. meleagris*, *A. hispidus*, *Arothron* sp.

Fifth Trophic Level

(Quaternary Consumers; Roving Carnivores)

Family Carcharhinidae (gray sharks)—*Carcharhinus melanopterus*, *C. menisorrhynchus*; Family Triakidae (smooth dogfishes)—*Triaenodon obesus*; Family Sphyraenidae (barracludas)—*Sphyraena genie*; Family Scombridae (tunas)—*Gymnosarda nuda*, *Katsuwonus pelamis*, *Euthynnus affinis*, *yaito*.

THE FOOD WEB

Figure 9 depicts in summarized form an overall picture of Marshallese food chains. For the sake of brevity various foraging activities have been combined under inclusive categories such as "algal feeders," etc. The reader is referred to earlier portions of the text for the specific constituents of these generalized categories. It is to be noted that only the major food pathways are shown in this food web, this being done for simplicity's sake because of the large number of species studied.

SUMMARY

1. Major gaps in our knowledge of coral reef ecology lie in our understanding of the taxonomic composition of the reef biota, the nature of biotic interaction between various trophic levels, and the specific community relationships obtaining in the several physiographic areas of a coral reef.

2. The present study attempts to fill these gaps by reporting upon the food, feeding habits, and ecological relationships of Marshallese fishes. The study was conducted at Bikini, Arno, and Eniwetok Atolls during the period 1947-1955. The geographical and physical aspects of these three atolls are described in detail along with descriptions of the various types of reefs encountered at each.

3. Fish examined for this study were obtained primarily by rotenone poisoning, with supplementary techniques (spears, hook and line, explosives) being used when warranted. Data recorded for each specimen were: standard length, sex, gonadal development, nature of alimentary tract, dentition, and type of food ingested. Over 2,000 individual stomachs were examined for the food study, and supplementing the laboratory work were hundreds of hours of underwater observation. We believe that combining the laboratory studies with the field observations enables us to present natural interpretations for the various ecological situations studied.

4. A discussion of food and feeding habits is presented for 56 families, 127 genera, and 233 species of Marshallese fishes, these figures representing more than half of the genera and somewhat less than half of the species known from the area. In addition to a discussion of each species, there are summaries by family and occasionally by genus.

5. The feeding habits of the species examined are categorized by foraging method as follows: algal feeders (consumers of unicellular algae, grazers, browsers, incidental algal feeders), detritus feeders, scavengers, zooplankton feeders, carnivores (feeders on fossorial, benthonic, and mid-water fauna, resident and transient roving carnivores), coral polyp feeders (browsers, grazers, and feeders on branching coral tips), and omnivores (facultative and incidental). Items frequently regarded as inedible (corals, echinoderms, sponges) were found to constitute significant portions of the diets of several fish groups.

6. The characteristic associations between fish and various coral reef habitats are illustrated and described for the following situations: supra- and intertidal pools, seaward reef flat, surf zone and surge channels, rocky and compacted sand substrates bearing algae, ledges and caverns, mid-water and surface communities, and glomerate and ramose coral heads and their bases.

7. The fishes considered are assigned to trophic levels as follows: primary consumers (herbivores), secondary and tertiary consumers (carnivores), and quaternary consumers (roving carnivores). Herbivorous species dominate Marshallese reefs because of favorable energetics between them and the great primary producer reef biomass. The more advanced fishes (trigger fish, puffers, surgeon fish, etc.) are typically members of the lower trophic levels, whereas the more primitive forms are carnivorous and frequently rank at the highest trophic levels.

8. A food web depicting energy flow in a coral reef ecosystem is presented.

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